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A Description of the Juvenile Phase Colour Patterns of 24 Parrotfish Species (Family Scaridae) from the Great Barrier Reef, Australia

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ABSTRACT. The juvenile colour patterns of 24 of the 27 parrotfish species presently recorded from the Great Barrier Reef are described. Two from the subfamily Sparisomatinae: *Calotomus carolinus* (Valenciennes) and *Leptoscarus vaigiensis* (Quoy & Gaimard). Twenty two from the subfamily Scarinae: *Bolbometopon muricatum* (Valenciennes); *Cetoscarus bicolor* (Rüppell); *Hipposcarus longiceps* (Valenciennes); *Scarus altipinnis* Steindachner; *Scarus bleekeri* (de Beaufort); *Scarus chameleon* Choat & Randall; *Scarus dimidiatus* Bleeker; *Scarus flavipectoralis* Schultz; *Scarus forsteni* (Bleeker); *Scarus frenatus* Lacepède; *Scarus ghobban* Forsskål; *Scarus gibbus* Rüppell; *Scarus globiceps* Valenciennes; *Scarus longipinnis* Randall & Choat; *Scarus niger* Forsskål; *Scarus oviceps* Valenciennes; *Scarus psittacus* Forsskål; *Scarus rivulatus* Valenciennes; *Scarus rubroviolaceus* Bleeker; *Scarus schlegeli* (Bleeker); *Scarus sordidus* Forsskål; *Scarus spinus* (Kner). Descriptions are given of the ontogeny of the colour patterns, where possible, from early post-settlement to the transition to the initial phase. Descriptions are based on field observations with additional colour notes on fresh and preserved specimens. Meristic data are also provided. Particular emphasis is placed on the size related ontogeny of colour patterns, with additional notes on short-term behavioural changes. The descriptions are intended for field identification of juvenile scarids; a rapid field identification guide and ecological notes on each species are given to facilitate field identification; specific notes for distinguishing species in the field are included. All species can be identified to the species level with the exception of two pairs of closely related species: *S. rivulatus* - *S. globiceps* and *S. psittacus* - *S. schlegeli*. Colour plates of live and/or fresh specimens of 22 species are given, sequential colour pattern changes are shown for some species. Most juvenile scarids share a common series of colour pattern changes during the early post-settlement period. These patterns are described and figured, and exceptions noted. Juvenile scarids likewise share a typical pattern of stripes and/or bars. The standard patterns are described and used as a basis for describing intraspecific differences in colour patterns.The juvenile colour patterns are discussed in relation to species complexes and adult relationships. The functions of juvenile colour patterns in relation to the ecology of juvenile scarids are also discussed. Two associations are described: schooling species bearing uniformly pale or striped patterns and solitary species with complex patterns.

BELLWOOD, D.R. & J.H. CHOAT, 1989. A description of the juvenile phase colour patterns of 24 parrotfish species (family Scaridae) from the Great Barrier Reef, Australia. Records of the Australian Museum 41(1): 1-41.

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The Scaridae is a distinctive family of herbivorous coral reef fishes, a prominent feature of which is the striking pattern of colour changes observed in most species. Most scarids display three distinct colour phases: a juvenile phase, an initial phase and a terminal phase, with the latter two phases corresponding to sexual stages in their protogynous life history. These three colour phases are usually distinct.

The changes in colour pattern throughout the life history of scarids have resulted in considerable taxonomic confusion. Only in the last decade have an increased knowledge of sexual ontogeny and detailed field observations on reproductive behaviour provided a reliable basis for linking the sex-related colour phases in many species. Extensive collections have helped resolve many of the problems associated with closely related species complexes distributed across wide geographic areas. Despite these advances, however, the juvenile phase of most species remains either poorly described or unknown.

One of the first steps towards an understanding of the structure and dynamics of reef fish populations is the ability to identify species during the early post-settlement and juvenile phases. Recent studies of the ecology of coral reef fishes have emphasised the importance of settlement and early post-settlement events in determining the structure of reef fish communities. Although scarids are a major component of the herbivorous reef fish community, the biology of juvenile scarids is poorly understood. This is primarily a result of taxonomic difficulties. It is important that this taxonomic impediment be overcome so that studies of the biology of juvenile herbivorous reef fishes may benefit from reliable species identifications of juvenile scarids. An identification guide is therefore a prerequisite to future studies of this group.

Despite the number of taxonomic studies on adult scarids no previous studies have focused solely on the identification of juvenile scarids. Descriptions of the juvenile colour phases of many species are lacking. Some descriptions, as in Schultz (1958), are based on museum specimens and are therefore of limited use for field identifications. A few descriptions of juvenile scarids in recent publications have been accompanied by colour plates and/or notes on the live colouration, but these descriptions are restricted to moderately large specimens.

The problems of identifying juvenile scarids are distinct

from those faced when identifying adults. The external morphology and meristic counts of most scarid species are extremely similar. This is a problem in adults but is further exacerbated in juveniles as many diagnostic characteristics, such as canine teeth or caudal fin extensions, are not developed. Descriptions must therefore be based primarily on colour patterns. Although there are no sex-related differences in juvenile colour patterns, most species do undergo marked changes during the juvenile phase. Descriptions of the colour patterns of variously sized juveniles are therefore of primary importance for field identifications. As the criteria used to distinguish juveniles differ from those used to separate adults, the two life stages need to be considered separately. This study therefore, specifically addresses the problem of identifying juvenile scarids.

In a study of the scarids of the Great Barrier Reef, Choat & Randall (1986) described the adult colour phases of 27 species. Descriptions of the juvenile phase of some species were included but these were typically of specimens larger than 50mm SL. In the present study, the descriptions are concentrated on the identification of juveniles during the early post-settlement period, with notes on the ontogeny of the colour patterns, where possible, from settlement to the initial phase. The present study is primarily restricted to a single geographic region, the Great Barrier Reef, although many of the species are present throughout the Indo-Pacific. Twenty four of the 27 scarid species recorded from the Great Barrier Reef by Choat & Randall (1986) are described. Juvenile specimens of the three remaining species *Calotomus spinidens* (Quoy & Gaimard), *Scarus frontalis* Valenciennes and *Scarus pyrrhurus* (Jordan & Seale) were not observed in the field or represented in collections from eastern Australia. Species designations follow Choat & Randall (1986), who provide a synonymy of each species and notes on their geographic distributions. The present study is primarily aimed as a guide for field identifications based on colour notes, colour plates and field observations. Additional notes on meristics and colour in alcohol also enable most species to be identified in preserved collections.

Materials and Methods

The main study and collection areas were on reefs around Lizard Island (14°40'S, 145°28'E), a continental island 30 km from the mainland and 18 km from the outer barrier reef. Lizard Island has a typical midshelf assemblage of herbivorous reef fishes (Choat & Bellwood, 1985; cf. Williams, 1982; Russ, 1984). Additional specimens were observed and collected by both authors from several other reefs in the vicinity of Lizard Island, Cairns and Townsville. The senior author also observed and collected specimens from the Central Visayas, Philippines; the junior author from the southern Great Barrier Reef (GBR). The study period extended from June 1981 to January 1984, with field work being concentrated during November to January (the peak settlement period). Field observations were made using SCUBA, with notes recorded on PVC sheets. Size and individual variations in colour patterns or the presence of scars enabled individuals of some species to be recognised for periods up to two years. Schooling species or those with variable colour patterns were tagged using subcutaneous injections of paint, following the technique of Thresher & Gronell (1978). Several species were maintained in aquaria for up to ten weeks to follow changes in their colour patterns during ontogeny.

Specimens were collected using a variety of techniques. Individuals under 11 mm SL were collected using small (220 x 125mm), clear self-seal polythene bags. Individuals between 11 and 35mm SL were captured using large, clear polythene bags (940 x 615mm). These bags were used as traps, with the mouth held open by coral or coral rubble. This technique is most efficient for small specimens. Above 35 mm SL, specimens were either speared using a modified Hawaiian sling and multiprong spear or were caught using a small mesh (7 mm square) barrier net and hand-net. Specimens were fixed in 10% seawater-formalin and stored in 70% alcohol.

Photographic records were taken of representative specimens of each species using a modified version of the technique described by Randall (1961). Specimens were killed by placing them in a deep freeze. Immediately after death, they were placed on a polystyrene base. Their fins were raised and held in place by strips of polythene secured by pins and irrigated with 40% formaldehyde for approximately five minutes. Care was taken to keep the eye moist, but not fixed. The specimens were then photographed in a vertical photographic tank. All photographs were taken by the senior author unless stated otherwise.

In the present study, settlement refers to the process of postlarval individuals moving from the plankton to the reef. Recently settled individuals are usually 8 to 10 mm SL and have incomplete pigmentation. The term juvenile refers to immature individuals, from 10 mm SL to the size at which they display the full initial phase colouration. Immature individuals with the full initial phase colouration are referred to as subadults. The size at sexual maturity varies from 67 to at least 315 mm SL, depending on the species, but is usually between 100 to 140 SL. The term initial phase (IP) refers to subadult and adult females, and primary males; terminal phase (TP) refers to secondary males or colour transformed primary males. A key and descriptions of the IP and TP colour phases of all GBR scarid species are given in Choat & Randall (1986).

Diagnostic meristic data include the number of median predorsal scales, the number of cheek scale rows, the number of scales in the ventral cheek scale row, and the number of pectoral fin rays. Median predorsal scales are counted from the most anterior scale. The form of small lateral or overlapping scales anterior to the first median predorsal scale and the relative sizes of the median predorsal scales are also noted. Cheek scale rows are horizontal scale rows between the lower edge of the orbit and the horizontal margin of the preoperculum. Counts of the pectoral rays included the upper rudimentary ray which is unbranched. No distinction is made between the

upper two unbranched rays and the remaining branched rays. All lengths refer to the standard length (SL), the straight-line distance from the tip of the snout to the base of the caudal fin.

The identification of preserved specimens is often dependent upon both scale counts and the pattern of the scales. The form of the median predorsal scales, in particular, is often diagnostic. The various median predorsal scale patterns are summarised in Fig. 1. Scale sizes are measured from the base of the scale or the posterior edge of the preceding scale to the posterior edge of the scale. Small lateral or overlapping scales anterior to the first median predorsal scale are identified but are not included in the median predorsal scale count.

The scale counts of all species increases during the early postsettlement period. The median predorsal scales are usually apparent at about 13 mm, with the full complement of scales developing simultaneously. Cheek scales are apparent at 14 mm and increase slowly in number, with scales developing anteriorly. The third or ventral row is the last of the rows to develop. The full complement of cheek scale rows is present at 20 mm.

In most species, the scale counts of specimens greater than 20 mm are indistinguishable from those of larger juveniles and adults. In some species, the relative size of the scales may change. For example, the first median predorsal scale is largest in juvenile *S. psittacus* and *S. schlegeli* whilst the second scale is largest in adults. The embedding of the anterior cheek scales recorded in adult *B. muricatum* and *C. bicolor* does not occur during the

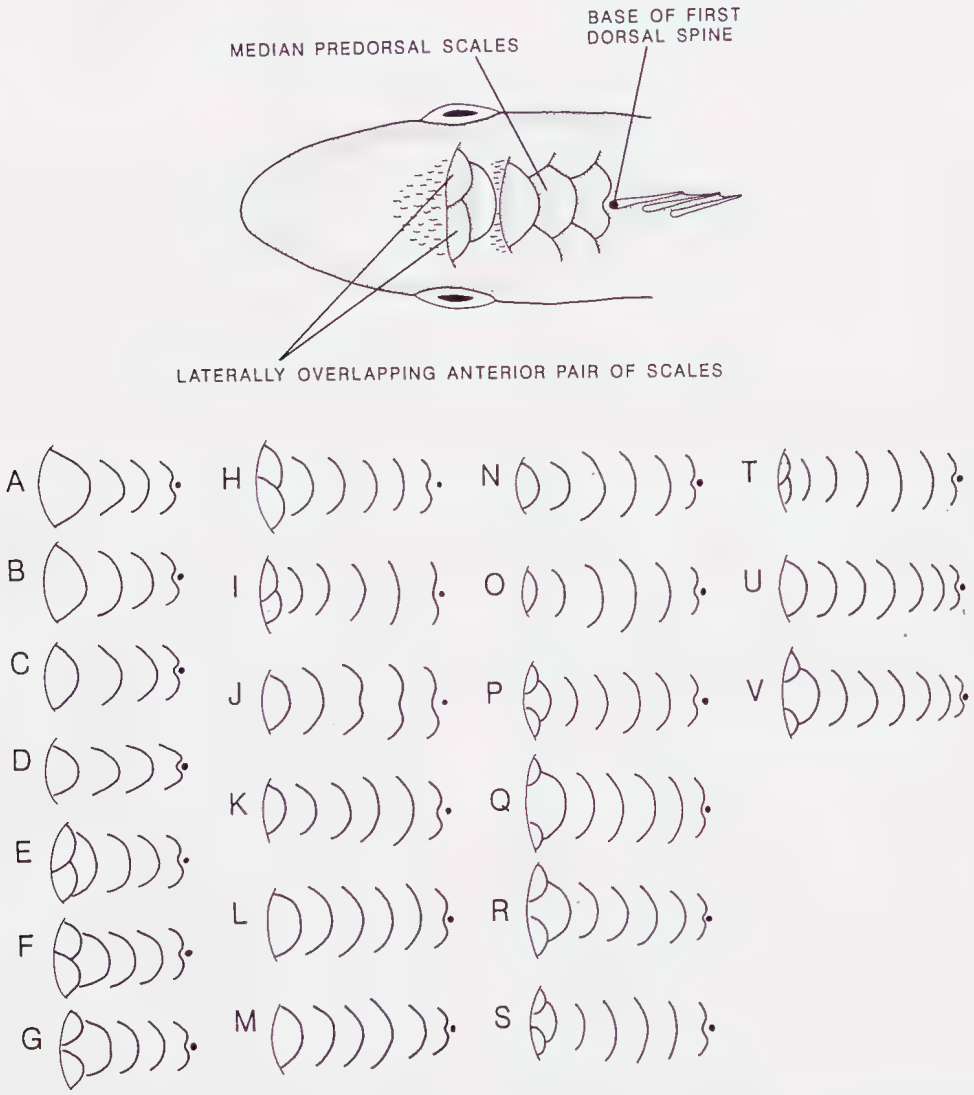


Fig.1. Variations in the form of the median predorsal scales of juvenile scarids from the Great Barrier Reef. *C. carolinus* - A; *L. vaigiensis* - D; *C. bicolor* - K,N; *B. muricatum* - J; *H. longiceps* - A,(B); *S. altipinnis* - O; *S. bleekeri* - B,(A); *S. chameleon* - F,(G,H); *S. dimidiatus* - M,O,(U); *S. flavipectoralis* - A; *S. forsteni* - T,(I); *S. frenatus* - M,R,(U,V); *S. ghobban* - O,(S); *S. gibbus* - B,(A); *S. globiceps* - I,(J,Q,L); *S. longipinnis* - A,C; *S. niger* - U,(M,Q,V); *S. oviceps* - *M,O,(P);* *S.psittacus* - A; *S. rivulatus* - O,L,(T,I); *S. rubroviolaceus* - N; *S. schlegeli* - A; *S. sordidus* - A,(B); *S. spinus* - E. Letters in parentheses refer to the occasional occurrence of unusual scale forms.

juvenile phase.

Voucher specimens were deposited in and specimens examined from the Australian Museum, Sydney (AMS); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Species Descriptions

The species descriptions are in alphabetical order. Each description follows a standard format.

MATERIAL EXAMINED provides reference numbers and details of the preserved specimens examined in this study. In addition, numerous freshly collected specimens were examined.

The DIAGNOSIS is based solely on material examined in this study. The terminology follows that of Choat & Randall (1986). All lengths refer to the standard length (SL). Unless stated otherwise, all specimens have white dental plates, no canine teeth, lips which cover the dental plates, and a rounded caudal fin.

DIAGNOSTIC COLOUR NOTES are a summary of the main diagnostic or characteristic features of the colour pattern of the species. It is intended as a rapid guide for field identifications.

COLOUR NOTES are a detailed description of the ontogeny of the colour patterns over as large a size range as possible, based primarily on field observations, with additional observations on freshly collected specimens and live fish in aquaria. Unless otherwise stated all observations refer to GBR material. In addition to the colour patterns described, all species displayed a mottled pattern at night or when severely stressed. The colour patterns of most species fade upon capture and remain faded in captivity. In the colour descriptions, stripes are longitudinal markings and bands are vertical markings; broad bands may be referred to as bars. The pale regions between dark stripes or bands are referred to as interspaces.

COLOUR IN ALCOHOL descriptions are based on material examined in the present study; all material had been stored in alcohol for at least three months.

ECOLOGY describes the typical behavioural and distributional characteristics of the species which will aid in field identification. Unless otherwise stated, all observations were made at Lizard Island.

FIELD IDENTIFICATION discusses specific aspects of the behaviour or colour patterns of the species which are most important in field identification. This section emphasises those characteristics which enable the species to be distinguished in the field.

PREVIOUS DESCRIPTIONS refer to previous descriptions of the juvenile colour phase. Species synonymies are given in Choat & Randall (1986). In addition to the descriptions noted, the colour patterns of several GBR scarid species during the late juvenile phase (greater than 50 mm SL) are described briefly and figured by Choat (1969) and Choat & Randall (1986). A description of the ontogeny of the juvenile colour patterns of most GBR species is given in Bellwood (1986).

Field Observations

Field identifications were based on both behaviour and colour patterns. The behaviour is of particular value in separating recently settled scarids and labrids. *Scarus* species settle at about 7.5 to 8 mm. They have a characteristic form of swimming, especially when disturbed, with the rear part of the body curled into a 'C'-shape. In this position, they drift from cover to cover propelled by their pectoral fins, periodically reversing the flexion of the body. Labrids may curl in a similar manner, but typically do so for much shorter periods of time. Labrids primarily swim in short spurts with the body remaining straight, or with a slow undulating motion. Some species (e.g. *Coris variegata*) occasionally oscillate vertically between spurts of movement. The 'C'-shaped position was displayed by all *Scarus* species observed. This behaviour ceases at about 11 to 12 mm SL after which a typical labriform swimming motion predominates. The swimming motion of *Leptoscarus, Calotomus, Cetoscarus* and *Hipposcarus* differs from *Scarus* species and is described in the species descriptions. Solitary or schooling behaviour is relatively consistent within a species and aids in field identifications. In addition, many species have restricted or characteristic distributions. These differences aid in field identifications and are summarised in Fig. 2. A more detailed description of the ecology of each species is given in the species descriptions.

Colour Patterns

All the species of *Scarus* examined shared a common colour pattern. This is most apparent shortly after settlement but varies in extent between species. Recently settled scarids have a transparent body with a row of pale dots along the base of the dorsal and anal fins and onto the caudal peduncle (Fig. 3A). Shortly thereafter, two additional rows are apparent on either side of the midline (Fig. 3B, Pl. 5B). The pattern of dots forms both vertical and horizontal rows. As the fish grows, the areas between the rows of pale dots darken particularly along the horizontal rows (Fig. 3C). This results in four dark dashed lines (Fig. 3D).

Depending on the species, these dashes may either fuse to form dark longitudinal stripes (with the medial rows fusing first) as in *S. gibbus, S. psittacus* and *S. rivulatus*, or subdivide to produce further dashed lines which then fuse, as in the dorsal stripe of *S. sordidus* and *S. spinus*. Alternatively, the dashes may become diffused and form vertical bands as in *S. dimidiatus* and *S. longipinnis*. These patterns are not fixed as individuals of several species display both striped and vertically banded patterns or a mixture of the two, as in *S. frenatus* (Pl. 5C) and *S. rubroviolaceus* (Pl. 3F, G). *S. niger* is an exceptional species in that although the pale dots are apparent, the dashed lines do not form. In this species, the characteristic

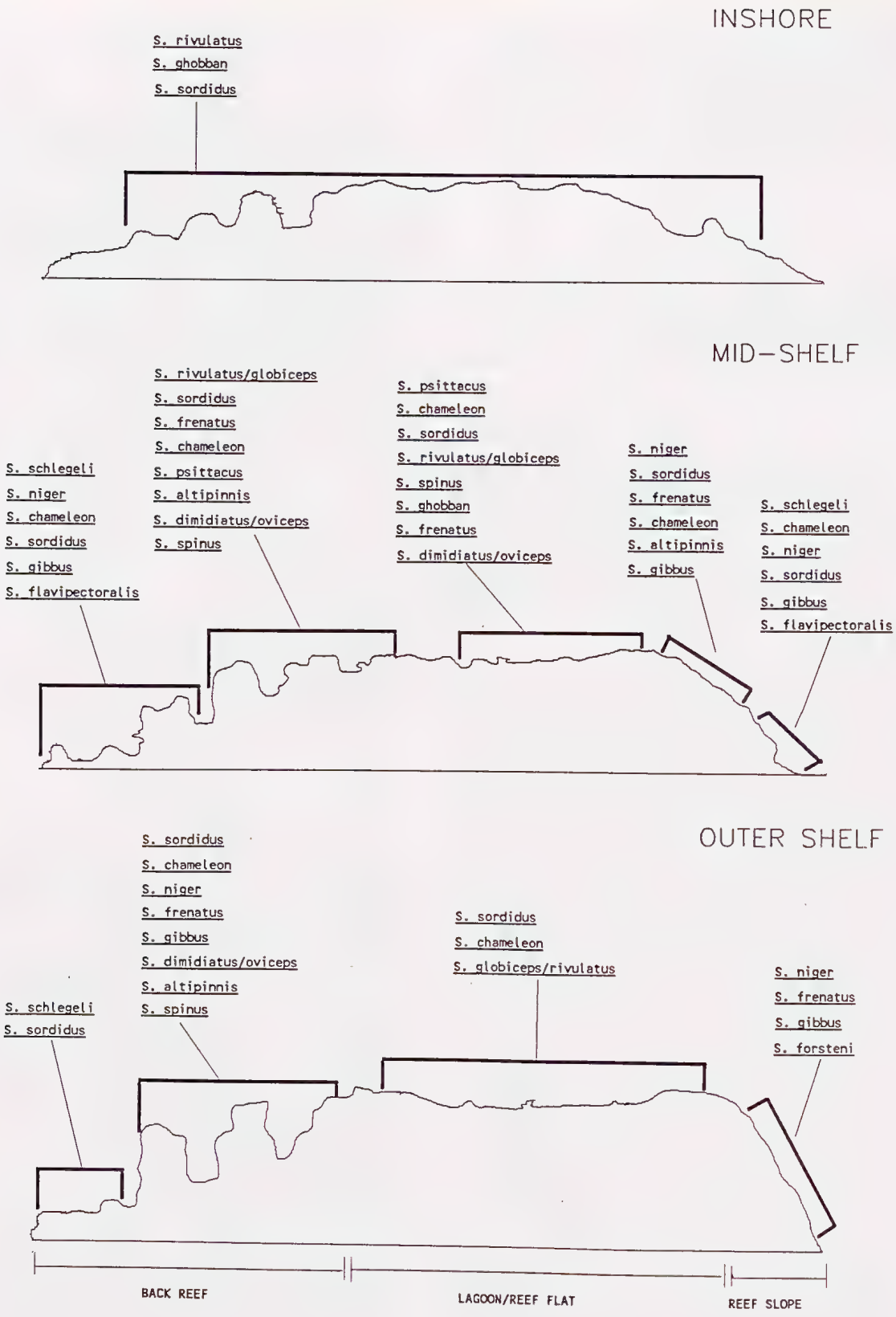


Fig.2. General distribution and abundance of juvenile scarids on reefs across the Great Barrier Reef, Australia. Species are listed in order of decreasing abundance. Distributions may vary markedly between reefs. The overall abundance of juvenile scarid is low on inshore reefs and extremely low on the outer slopes of outer shelf reefs.

dark ventral surface and pale spots develop shortly after settlement (Pl. 5E). The pale dots are lost with increasing size in most species, but remnants are retained in *S. rubroviolaceus, S. forsteni, S. altipinnis* and some colour patterns of *S. sordidus*.

The fusion of the four longitudinal dashed lines produces four dark body stripes. These are designated here as the dorsal, orbital, pectoral and ventral stripes (Fig. 4A). The dorsal stripe extends from the dorsal part of the snout, passes along the dorsal flank, near the base of the dorsal fin and terminates either at the posterior extremity of the dorsal fin base or on the dorsal edge of the caudal peduncle. The orbital stripe arises on the snout, passes through the orbit and terminates on the dorsal part of the caudal peduncle at the base of the caudal fin. The pectoral stripe extends from the lower jaw articulation, passes over the cheek, through the pectoral fin base and terminates on the ventral part of the caudal peduncle at the base of the caudal fin. The ventral stripe extends from the base of the operculum (in the interopercular region), passes along the ventral flank (belly) and terminates either at the base of the anal fin or on the ventral edge of the caudal peduncle. Pale spots which correspond with the pale dots found in recently settled and early dashed phase individuals may remain in either the dark stripes or the pale interspaces.

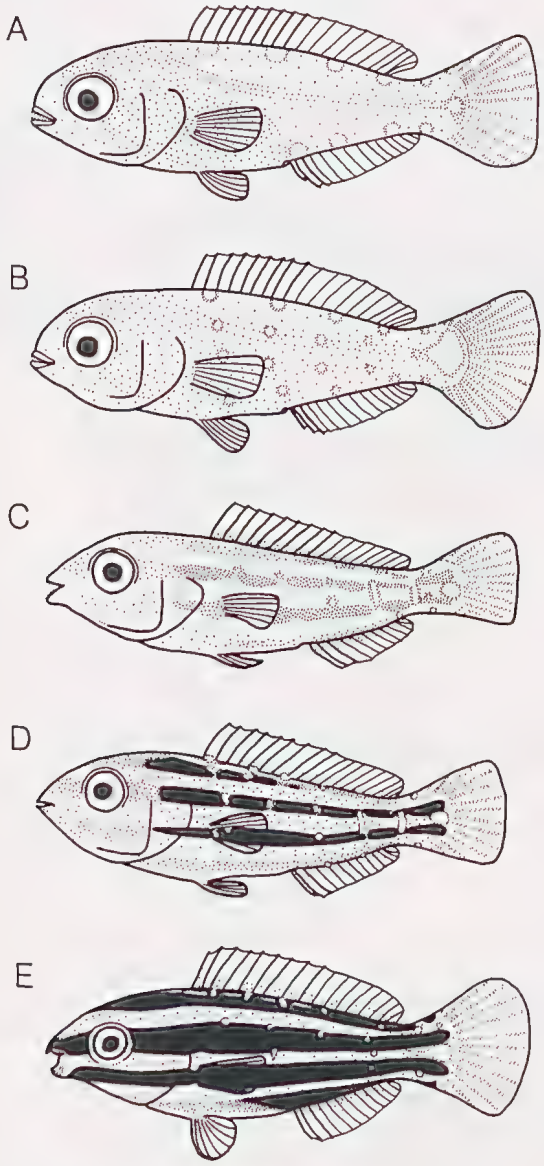


Fig.3. Ontogenetic changes in the colour pattern of juvenile *Scarus* species, leading to the formation of the four primary stripes. This figure is based primarily on the ontogeny of *Scarus frenatus* and *S. spinus*. Approximate lengths: (A) 9-10 mm SL; (B) 10-11 mm SL; (C) 11-13 mm SL; (D) 13-16 mm SL; (E) 20 mm SL.

Most *Scarus* species possess the four primary juvenile stripes, although there is some degree of between-species variation in the form, location, size and intensity of these stripes. The main variation in form is found in the dorsal stripe. As noted above, it may divide during the dashed phase to produce two stripes. In this situation, the ventral division remains in the normal dorsal stripe position, whereas, the dorsal division arises from a point between the orbits and passes along the midline at the base of the dorsal fin, before fusing with the ventral division at the posterior base of the dorsal fin (Fig. 3E). When viewed from above, the dorsal division appears as a single stripe running along the base of the dorsal fin.

Variation in the location of the stripes is also most notable in the dorsal stripe. In most species, there is a distinct gap between the dorsal stripe and the base of the dorsal fin, although in some species the dorsal stripe remains relatively close to the base of the dorsal fin, as in *S. rubroviolaceus* and *S. frenatus*. Variations in the size and intensity of the stripes are complex, often as a result of changes during ontogeny. However, in some species, the size and intensity may be diagnostic or characteristic, as in *S. rubroviolaceus* and *S. psittacus*.

It should be noted that the stripes described above are lost with growth and are not related to the scale row stripes that are present in the IP of some species (e.g. *S. frenatus*).

As with juvenile body stripes, vertical bands, if present, have a 'typical' *Scarus* pattern (Fig. 4B), which reflects the pattern of pale dots found in recently settled and small dashed phase individuals (as in *S. oviceps*, Pl. 4B,C; *S. longipinnis*, Pl. 3D, and *S. schlegeli*, Pl. 2G,H). The maximum number of vertical bands displayed by most species is six (seven dark vertical bands only in *S. longipinnis*, Pl. 3D). The first band passes from the region of the first dorsal spine to the base of the pelvic fin, passing through the base of the pectoral fin. The second band passes from the dorsal fin to an area midway between the pelvic fins and anal fin, occasionally extending to the first spine of the anal fin. In species with seven bands, it is the second band that subdivides dorsally to produce the extra band. The third band passes from the midposterior part of the dorsal fin to the midanterior part of the anal fin. The fourth band connects the posterior regions of the dorsal and anal fins. The fifth band crosses the caudal peduncle, and the sixth band lies at the base of the caudal rays. This band may be triangular in shape with an anteriorly pointing apex.

Between each vertical band, the pale interspaces follow the pale dots described in newly settled and early dashed

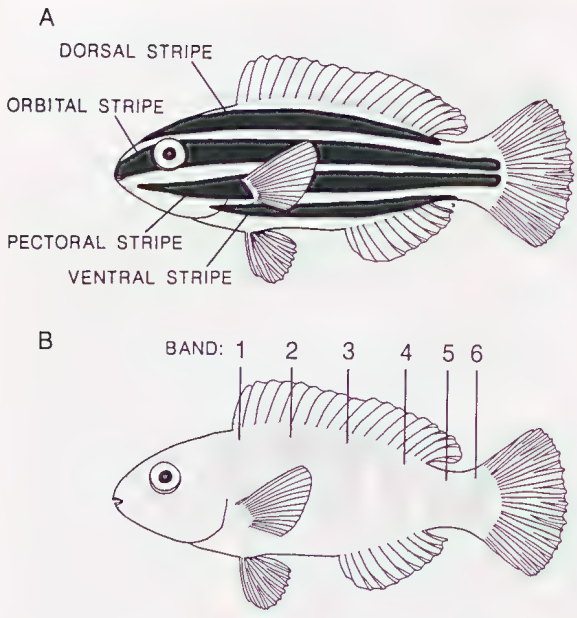


Fig.4. The 'typical' colour patterns of a juvenile *Scarus* species showing: (A) the four primary scarid stripes and (B) the six primary scarid bands.

phase individuals. These pale dots frequently remain as pale highlighted areas in larger juveniles. In some species (e.g. *S. ghobban* and *S. schlegeli*), these interspaces are relatively narrow and give and overall appearance of thin pale vertical bands on a darker background. The vertical bands may be straight as in *S. bleekeri* and *S. ghobban*, but in most species, they have a medial curve or flexion. The bands typically extend over the dorsal and ventral halves of the body, but may be lost ventrally as in *S. dimidiatus* and *S. oviceps*. As with juvenile stripes, the full number of vertical bands is not always present. The bands may (a) represent one of a series of colour patterns as in *S. chameleon*, (b) be combined with other patterns as in *S. rubroviolaceus*, or (c) be incompletely formed as in *S. dimidiatus* and *S. oviceps*. The bands on the caudal peduncle, in particular, are often poorly developed or absent as in *S. schlegeli, S. bleekeri, S. dimidiatus* and *S. oviceps*. Vertical bands are retained in the IP of some species (e.g. *S. bleekeri, S. dimidiatus, S. ghobban, S. longipinnis, S. oviceps, S. schlegeli* and *S. spinus*).

The length of the juvenile phase varies widely between species. In *S. ghobban* and *S. spinus*, the juvenile phase lasts for only a short while. The loss of juvenile phase colour patterns at 90 and 40 mm respectively, represents only 16 to 18% of the maximum length for each species. In contrast, specimens of *S. frenatus* and *C. bicolor* with distinct juvenile colour patterns may be recorded up to 100 and 150 mm respectively. This represents 30 to 33% of the maximum size attained by these species.

A Rapid Field Identification Key to Juvenile Scarids from the Great Barrier Reef, based on the Diurnal Field Colouration of Specimens between 20-60mm SL

1. Body white with single broad band over eye, black ocellus in dorsal fin.....*Cetoscarus*

—— Body not white, no band through eye, no ocellus in dorsal fin.....2

2. Single pale beige horizontal line from orbit terminating in a black dot at base of caudal fin, snout angular.....*Hipposcarus*

—— No single pale beige line from orbit ending in a distinct dark dot, snout not angular.....3

3. Body with series of dots, irregular flecks, bands, mottling, body not uniform or with longitudinal stripes, dorsal and anal fins may have distinct flecks..... .....(*Calotomus, Leptoscarus, Bolbometopon, Scarus* spp.) 4

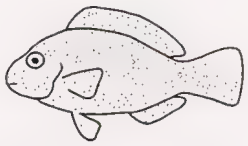
—— No flecks, bands or mottling, dots if present few in number and restricted within stripes, body with uniform colour or two or more longitudinal stripes, fins not distinctly mottled.....(*Scarus* spp.) 11

4. Small pale dots on body numerous, in irregular rows and/or in 2-3 even rows of 4-6 dots.....5

—— Pale dots either few and irregular or absent, pale flecks in vertical lines may be present.....7

5. Uniformly green-brown body; 2-3 rows of clear pale dots, no dark dots on caudal peduncle.....6

—— Dorsum olive; black ventrally with numerous small white to blue-white dots, two distinct dark dots on caudal peduncle.....*S. niger*



6. Deep body, (depth < 2.6 in SL), 2-3 rows of pale dots without additional small dots or flecks.....*Bolbometopon*

—— Elongate body, (depth > 3.0 in SL), 2-3 rows of pale dots and numerous smaller dots on body, fins with numerous small dots or flecks, occasionally single pale longitudinal stripe.....*Calotomus/Leptoscarus*

7. Body and fins with dark and pale flecks, no dark vertical bands; caudal fin and caudal peduncle pale.....*S. altipinnis/frenatus*

—— Body without dark and pale flecks; with dark vertical bands, caudal fin and caudal peduncle same colour as body.....8

8. Body bright yellow with 2-4 dark bands usually restricted to dorsum.....*S. dimidiatus/oviceps*

—— Body not bright yellow, vertical bands usually extending onto ventral half of body.....9

9. Bands approximately same width as pale interspaces.....*S. longipinnis*

—— Pale interspaces much narrower than bands.....10

10. Body dark brown-black with pale grey-brown interspaces.....*S. schlegeli*

—— Body pale tan, occasionally with orange hue, paler interspaces white with blue hue.....*S. ghobban*

11. Body brown to black or with brown or black stripes.....12

—— Body tan, pale grey, olivaceous to pale brown, with or without stripes.....16

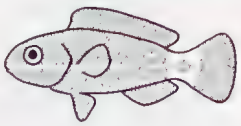
12. Body and caudal peduncle uniformly dark brown-black.....*S. bleekeri, S. gibbus, S. schlegeli, S. sordidus,* or in deep water, *S. chameleon* or *S. longipinnis*

—— Body with pale interspaces between dark stripes or caudal peduncle with pale patches.....13

13. Caudal peduncle pale off-white.....14

—— Dark body stripes extend onto caudal peduncle.....15

14. Caudal peduncle and caudal fin uniformly off-white.....*S. bleekeri*



—— Caudal peduncle and base of caudal fin off-white with dark dot in centre of caudal peduncle.....*S. sordidus*

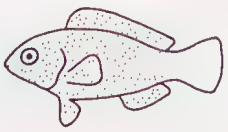
15. Broad black stripes on body, stripes on caudal peduncle fusing with dark caudal fin base, all vertical fins dark at bases.....*S. gibbus*

—— Dark orbital and pectoral stripes usually terminating in intense dark black dots, fins mottled or pale hyaline grey.....*S. sordidus/spinus*

16. Body uniformly coloured.....17

—— Body with horizontal stripes.....19

17. Caudal fin and caudal peduncle same colour as body.....18



—— Caudal fin and caudal peduncle with pale yellow hue, body olive tan to grey brown.....*S. rivulatus*

18. Body pale grey, tan or grey brown, abruptly pale off white below level of pectoral fin base.....*S. chameleon, S. psittacus* or *S. rivulatus*

—— Uniformly pale grey brown to brown.....*S. chameleon, S. flavipectoralis, S. forsteni, S. globiceps, S. psittacus, S. rivulatus*

19. Pale dots visible in dark stripes.....20

—— No pale dots in dark stripes.....22

20. Pale dot at tip of pectoral fin larger and clearer than the rest.....*S. forsteni*

—— Pale dots of approximately even size.....21

21. One dark band (No.2) usually visible behind pectoral fin, interspaces pale grey brown.....*S. rubroviolaceus*

—— No dark band visible, interspaces with metallic bronze hue.....*S. psittacus*

22. Body elongate; medial stripes (orbital and pectoral) distinctly broader and darker than dorsal stripe.....*S. flavipectoralis*

—— Body not elongate, 3 stripes clearly visible on body, medial stripes not distinctly broader and darker than dorsal stripe.....23

23. Pectoral stripe continues forward onto operculum.....24

—— Pectoral stripe not continuing forward of pectoral base.....*S. chameleon*

24. Orbital stripe slightly broader and darker than dorsal or pectoral stripes (dark cysts often on body).....*S. psittacus*

—— Dorsal, orbital and pectoral stripes of similar breadth and intensity.....*S. forsteni, S. ghobban, S. globiceps, S. psittacus, S. rivulatus, S. rubroviolaceus*

Calotomus carolinus (Valenciennes)

Pl. 1A

Material examined. (1 specimen: 43 mm). AUSTRALIA - Lizard Island, AMS I. 25905-002 (1:43 mm).

Diagnosis. Median predorsal scales 4, no anterior pair, scale size increasing anteriorly; 1 cheek scale row (4 scales); pectoral rays 13; jaws with incisiform imbricate teeth in oblique rows, not fused to form dental plates; body elongate, mouth pointed.

Diagnostic colour notes. Body and fins green to green brown with white and brown dots and flecks; white patch covering first 2 dorsal spines.

Colour notes. Colour patterns change little during juvenile phase, with no rapid colour changes; recently settled specimens (approximately 12 mm), body translucent with few brown and white dots in random pattern, white patch on anterior part of dorsal fin distinctly visible, extending from first dorsal spine to, but not including, third dorsal spine, remaining part of dorsal fin and other fins hyaline; greater than 13 mm (Pl. 1A), body darkens to grey green or green brown, dots and flecks increase in number, with double row of large pale dots along flank, and an indistinct row near dorsal fin base; these dots correspond with pale dots present in juvenile *Scarus* species (Fig. 3B); vertical fins grey green, flecked with brown and white, pectoral fins hyaline, white patch on anterior part of dorsal fin present to 43 mm (Pl. 1A), but lost by 80 mm, iris green. In progressively larger specimens, body darkens with browner hue, pale dots and flecks decrease in relative size and intensity; IP colouration complete at approximately 80mm.

Body form. Small specimens, body elongate, mouth pointed. Large specimens, body relatively deep, head rounded with protruding eyes which are distinctly visible when viewed from rear.

Colour in alcohol. At 31-43 mm, body pale green grey, nape brown, series of brown dots on body and along dorsal fin base, fins indistinctly mottled hyaline.

Ecology. Uncommon; solitary, occasionally in small multispecies schools; site attached when small. Recently settled specimens (12-13 mm) recorded over low algal covered coral rubble on sand, near reef slope base (7-10 m), North Reef, Lizard Island. Juveniles (15-100 mm) observed over coral rubble, coral rock and macroalgae, on or near reef slope base (5-11 m), in exposed and semi-exposed locations at Lizard Island. Moderately large juveniles (60-80 mm) recorded from reef slope (at 12-20 m) of Yonge Reef, an outer shelf reef.

Field identification. This is a member of the subfamily Sparisomatinae and is one of the more labrid-like scarids. In the field, it can be distinguished from other scarids by its unusual body form and colouration but may, when recently settled, be difficult to distinguish from some labrids. It settles at a relatively large size. The smallest transparent early postsettlement specimen observed was approximately 12 mm (cf. 7.5-8 mm in *Scarus* species). The swimming mode of *C. carolinus* is unusual when compared to that of other scarids. At 14-16 mm, it only occasionally moves with a 'C'-shaped body (a characteristic of *Scarus* species) and often swims in a labrid-like manner, i.e. in short bursts, with the body held straight. At 16-25 mm, the labrid-like swimming mode is retained. When disturbed, it often glides away, laying to one side with the dorsal and anal fins extended and the flank exposed to the onlooker. This swimming behaviour is similar to that of the labrid *Novaculichthys taeniourus* (Lacepède). At greater than 25 mm, however, *C. carolinus* swims in a more 'typical' scarid-like manner.

Previous descriptions. A colour plate of a 44.2 mm specimen from Taiwan in Burgess & Axelrod (1974, pl.283, p.995), provisionally identified as *Calotomus japonicus* (Cuvier & Valenciennes), is probably *C. carolinus*. Bruce & Randall (1985) describe and figure the late juvenile phase.

Leptoscarus vaigiensis (Quoy & Gaimard)

Pl. 1B

Material examined. (3 specimens: 30-35 mm). PHILIPPINES - Bantayan Beach, Dumaguete City, AMS I.27814-001 (1:30 mm), AMS I. 27812-001 (1:34 mm), AMS I.27813-001 (1:35 mm).

Diagnosis. Median predorsal scales 4, scales subequal, no anterior pair; 1 cheek scale row; pectoral rays 13; body elongate.

Diagnostic colour notes. Body olive green brown, dorsal, anal and pelvic fins hyaline with faint brown mottling; scale edges often dark; body either (a) uniform, (b) with a broad orbital stripe and narrow pectoral stripe, or (c) with 2-4 narrow dark stripes on the belly and flank.

Colour notes. 1 specimen, 50 mm, Sydney Harbour (Pl. 1B): body green brown, fading ventrally to off-white belly, 3 distinct series of 4-6 pale dots on body, 2 on midflank, 1 near dorsal fin base, dots correspond with pale dots on recently recruited *Scarus* species (Fig. 3B), medial fins mottled white and brown basally, hyaline distally, caudal olivaceous hyaline, pectoral fins hyaline.

A variable species, capable of rapid changes in its colour pattern; because of lack of detailed observations on GBR specimens, following notes are of Philippine specimens 30.5-38.5 mm. (A) Freshly collected: body olive green, belly and cheek off-white with golden sheen, especially on operculum and pectoral fin base, scales with dark edges,

iris pale silver, golden-orange near pupil, dorsal, anal and caudal fins hyaline brown, dorsal fin with 4 dark brownish patches basally, anal fin with 3 dark patches basally, scaled region of caudal fin green, pelvic fins hyaline with reddish-brown patch anteriorly, pectoral fins hyaline with very faint pink-brown hue. (B) In field: body olive-green brown, with broad dark stripe extending from snout through orbit, terminating in upper part of caudal peduncle, narrow pale interspace separates this stripe from narrow dark stripe which arises on cheek, passes through pectoral fin base, and terminates near posterior part of anal fin base (these stripes are comparable to orbital and pectoral stripes of *Scarus* species); may display stripe composed of fine tan mottling, arising abruptly in interorbital region, passing along dorsal fin base, and tapering to posterior end of dorsal fin base; belly off white, iris green to olive green with gold ring around pupil, dorsal, anal and pelvic fins hyaline with faint brown mottling, pectoral fins hyaline. (C) In captivity: as in field, except body and fins paler with green hue, 2 series of 5-6 pale dots on midflank become clearly visible (as in Pl. 1B), third row near dorsal fin base often indistinct, dorsum mottled with network of dark scale edges; 2-4 narrow dark stripes on flank and belly following scale rows, formed by dark dorsal and ventral scale edges; these stripes do not follow 'typical' scarid pattern (Fig. 4).

At greater than 38 mm, body remains olivaceous to grey green, series of relatively large pale dots lost but body peppered with small pale dots, especially ventrally; these dots increase in relative size throughout the juvenile phase; belly pale with 4 pale lines following scale rows, dorsal and anal fins hyaline with brown spines and rays, caudal fin hyaline with olive-green rays, pectoral fins with olivaceous hue, iris golden orange; faint mottling on body and fins becomes increasingly distinct during late juvenile stage, before gradual transition to IP colouration, which is complete at about 70 mm.

Colour in alcohol. At 30.5 mm, body pale-olive green with darker grey-green mottling; pale stripes in belly, series of pale dots on body, dark orbital stripe and grey brown and white mottling of unpaired fins clearly visible; at greater than 34 mm, body pale grey green dorsally, pale olive green ventrally, pale markings on body and fins not retained, pale grey-green mottling retained but indistinct, pale stripe from opercular margin (dorsal to pectoral fin base) to midcaudal peduncle indistinct (stripe corresponds to interspace between orbital and pectoral stripes).

Ecology. Not observed on GBR. In Philippines: solitary; moderately common in large dense shallow seagrass beds (0.5-3.0 m; *Thalassia* and *Cymodocea*), usually observed swimming between blades, probably settles in seagrass beds; when disturbed, juveniles swim in labrid-like manner, often in short bursts interspersed by stationary periods, hanging tail-down or laying among seagrasses; small juveniles appear to feed on seagrass epiphytes.

Field identification. This is one of the few scarid species found in seagrass beds. Its swimming mode and distinctive colouration distinguish it from all GBR *Scarus* species. It may, however, be confused with *Calotomus* species and some labrids. *L. vaigiensis* can be distinguished from labrids by its more rounded, shorter snout and distinctive colour pattern, and from *Calotomus carolinus* by its more elongate body, rounded snout, and lack of a white patch on the anterior part of the dorsal fin. The second *Calotomus* species, *Calotomus spinidens* is rare on the GBR (Choat & Randall, 1986), but in areas where this seagrass species is abundant, it can easily be distinguished from *L. vaigiensis* by its deeper body and a prominent pale stripe on the flank.

Previous descriptions. The field colour patterns of juvenile *L. vaigiensis* have not been described previously. Bruce & Randall (1985) describe the colour of juveniles in alcohol. This is a small species, which may mature at sizes as small as 69 mm (Robertson *et al.*, 1982). Only specimens below 69 mm are therefore considered juvenile.

Remarks. Despite its widespread distribution along the length of the GBR (Choat & Randall, 1986), *L. vaigiensis* was not observed on any of the GBR reefs examined. In the Philippines, juvenile *L. vaigiensis* were only recorded from seagrass beds. It is likely therefore, that juveniles may be observed in similar areas on the GBR. The single Australian specimen recorded in this study was observed among macroalgae in Sydney Harbour (R. Kuiter, personal communication). As this location is on the edge of the geographic range of the species, i.e. a sub-tropical region, its habitat location may be atypical.

Cetoscarus bicolor (Rüppell)

Pl. 1C

Material examined. (5 specimens: 11-96 mm). AUSTRALIA - Lizard Island, lost (1:11 mm); MICRONESIA - Kayangel Island, Palau, CAS 62588 (1:59 mm); PHILIPPINES - Sumilon Island, AMS I.27810-001 (1:36.5 mm), AMS I.27811-001 (1:56mm); SEYCHELLES - Mahe Island, CAS 58531 (1:96 mm).

Diagnosis. Median predorsal scales 6 (occasionally 7), posterior 4 largest; cheek scale rows 2-3, 0-6 in ventral row; pectoral rays 14; anterior dorsal spines elongate, especially in smaller specimens (greater than 2 times longest ray at 11 mm; 1.5 times at 36.5 mm; 1.3 times at 56 mm).

Diagnostic colour notes. Body white, with broad single brick-orange bar from anterior edge of orbit to origin of dorsal, bar edged in black; dorsal fin with large black ocellus with orange border; caudal fin margin orange; belly and pelvic fins with yellow hue.

Colour notes. The most distinctive and easily identified juvenile scarid; at 11-12 mm, body white, head brick red, fins hyaline, except first few spines of dorsal fin which are white, exceptionally long (greater than 2 times

longest ray) and usually held erect, dorsal ocellus absent; 30-40 mm, colour pattern dominated by broad vertical orange bar with black anterior and posterior margins, bar extending from anterior margin of orbit to base of first dorsal spine and pectoral fin, it does not correspond with bars found in *Scarus* species, body, mouth, snout, anterior part of dorsal fin and caudal fin white, caudal fin with orange posterior margin, anterior part of dorsal fin bearing large black ocellus with orange margin (Pl. 1C; N.B. fish viewed from rear); larger specimens (40-60 mm), orange margin of caudal fin extending along dorsal and ventral edges, white colouration in anterior part of dorsal and anal fins extending posteriorly, yellow colouration extending from pectoral base onto pelvic fins and belly to base of anal fin; at greater than 60 mm, orange bar slowly diffuses, body and fins darken, orange markings fade, ocellus decreases in relative size (as in 123 mm specimen figured in Randall & Bruce, 1983); at greater than 150 mm, bar almost completely lost, only diffuse brown patches remain, especially along outlines, body pale grey with scattered small darker dots, dorsal ocellus fades, fins pale grey; IP colouration complete at 180 mm.

Colour in alcohol. At 36-39 mm, body off white, grey to brown; orbital bar may be slightly darker; orange and yellow markings extremely faint or lost; black ocellus on dorsal and dark lines marking anterior and posterior edges of orbital bar remain distinct to at least 96 mm.

Ecology. Rare; solitary; site attached; settlement site of single individual recorded November 1980, in large piece of algal covered arborescent coral at base of semi-exposed reef slope, at North Reef, Lizard Island. Most juveniles observed amongst coral rubble and boulders, in gullies or near reef slope base, 3-11 m, typically in moderately exposed locations, including backreef bommies; a shy species, small specimens, in particular, remain close to substratum and rapidly dive for cover if disturbed, in contrast to flight of *Scarus* species.

Field identification. The striking colour pattern enables this species to be rapidly distinguished from all other scarids. The only possible confusion may be with *Amphiprion* species as noted below, however, the white body and lack of any association with an anemone clearly distinguish this species.

Previous descriptions. The juvenile phase of *C. bicolor* has been described as a new species on two occasions: as *Scarus ocellatus* by Valenciennes (in Cuvier & Valenciennes, 1840) and as *Scarus ophthalmistius* by Herre (1933). The juvenile of *C. bicolor* has subsequently been described by numerous authors, partially as a result of its popularity as an aquarium species. Scientific descriptions include those of Schultz (1958), Randall & Bruce (1983) and Choat & Randall (1986). Colour plates are given in Axelrod & Emmens (1969, pp. 247-248), Burgess & Axelrod (1972, pl. 271, p. 154; 1973a, pl. 348, p. 458; 1974, pls 260,261, p. 984; as *Bolbometapon bicolor*) and Masuda *et al.* (1984; pl. 212A). Many authors, especially those of popular aquarium books, place this species in the genus *Bolbometopon*. In the present study it is placed in the genus *Cetoscarus* following Randall & Bruce (1983) and Choat & Randall (1986). The status of this genus is currently under investigation.

Remarks. At 11 mm, *C. bicolor* swims in an undulating manner, strikingly similar to that of similarly sized *Amphiprion* species. This swimming behaviour is slowly lost with increasing size. With their undulating swimming mode, unusual colour pattern, and shy, cover seeking behaviour, recently settled *C. bicolor* bear a striking resemblance to recently settled *Amphiprion* species. This similarity may represent mimicry (Bellwood, 1986).

Bolbometopon muricatum (Valenciennes)

Fig. 5

Material examined. (12 specimens: 47-315 mm). AUSTRALIA - Lizard Island, GBR, AMS I.18755-077 (1:60 mm); LINE ISLANDS - Fanning Island, USNM 293162 (4:61-93 mm); MICRONESIA - Map Island, Yap Island, CAS 62586 (1:47 mm); Ponape Island, USNM 175268 (1:51 mm); Garayamo Island, Palau, CAS 62587 (1:67 mm); Koror Island, Palau, CAS 62584 (1:74 mm); Pelelio Island, Palau, BMNH 1874.11.16:5 (1:171 mm); Urukthapel Island, Palau, CAS 62585 (1:205mm); PHILIPPINES - Bais Bay, AMS I. 27865-001 (1:315 mm).

Diagnosis. Median predorsal scales 5 (occasionally 4), scales subequal, no anterior pair; 3 cheek scale rows, 2 (occasionally 1) in ventral row; pectoral rays 16; dental plates white; gill raker count ca. 20 (cf. 38-81 in Scarus species).

Diagnostic colour notes. At 315 mm, body and fins dark grey brown; numerous small brown dots on head, dorsum and vertical fins; distinct series of pale white dots on body, in 2-3 rows of 4-5 dots.

Colour notes. Body greenish with 3 series of 4-5 pale dots on flank, comparable to pale dots on recently settled *Scarus* species (Fig. 3B), vertical fins dark greenish, pectorals hyaline yellowish, pelvic fins greenish, iris yellow, white spots on body distinct to 300 mm. At 315 mm, (immature specimen, based on gonad status) freshly collected: body dark grey with brown hue, paler ventrally, scale edges brown in midbody, black posteriorly, each scale on dorsum with 1-3 (usually 1-2) brown dots one third pupil width, scales on caudal peduncle with dark area medially, series of pale orbit-sized dots on body, 2 distinct rows of 4-5 dots medially, 2 rows of 2-3 indistinct dots along dorsal fin base and between medial rows, dots in positions corresponding to those of recently settled *Scarus* species (Fig. 3B, cf. Pls 4F, 4G & 5B), forehead and snout dark grey, orbit, cheek and operculum grey with numerous brown dots and a few short undulating lines one third pupil width, cheek scales edged with brown, lower lip and chin with pale pink hue, iris brown medially, pale gold distally,

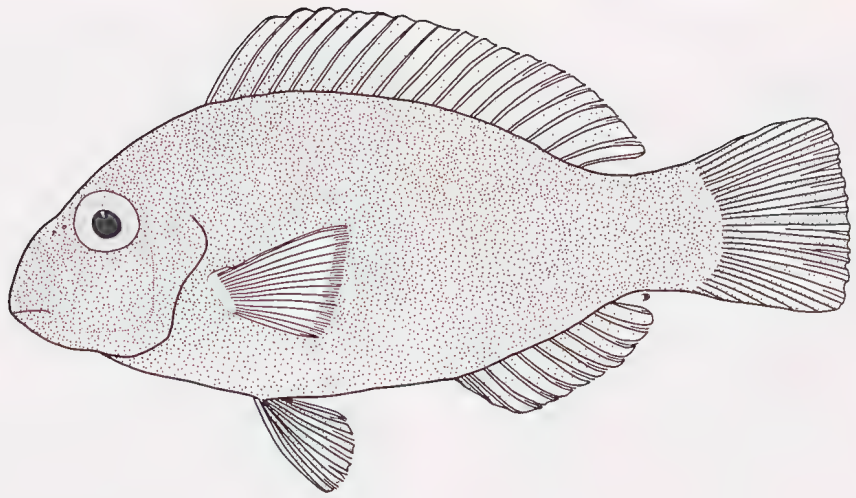


Fig.5. *Bolbometopon muricatum* 61 mm SL, 75.5 mm TL. Based on USNM 293162, Fanning Island, Line Islands.

dorsal, anal and pelvic fins grey with brownish-purplish hue, dorsal fin with few dark brown-black dots near base, anal fin with several indistinct brown dots half to one third pupil width, pelvic fin off white near belly, caudal fin black with numerous brown streaks in inter-ray areas, pectoral fin pale grey with brown streaks on dorsal half, fin base with 1-5 small black dots; in field, pale body dots lost by approximately 500 mm, greater than 500 mm body and fins uniformly grey green, as in adult specimens.

Body form. Small specimens 47-51 mm, body deep, maximum depth at first dorsal spine approximately 2.1 in SL, snout somewhat angular; forehead becomes steeper with increasing size, resulting in steep blunt profile at 205 mm; small hump on forehead first apparent at approximately 300 mm SL.

Colour in alcohol. Body pale brown to dark-grey brown, darkest dorsally, belly and anal fin palest, dorsal, anal, and pelvic fins hyaline brown grey to dark-brown grey, posterior edge of caudal fin rays often darker grey; 47-93 mm usually 15-50 small dark brown dots (less than one half times pupil width) scattered over body especially on dorsum; 75-315 mm, 3 rows of pale dots visible on flank as in live individuals.

Ecology. Very rare; only 1 juvenile specimen collected from GBR, from Lizard Island; junior author observed several solitary juveniles (250-300 mm) on Ellison Reef, an inner midshelf reef off Innisfail, Queensland.

On western Pacific reefs, several juveniles collected in shallow waters: 2 specimens in turbid waters 0-3 m, near mangrove vegetation at Yap and Palau Islands; 4 specimens in lagoon at Fanning Island and Ponape; 1 specimen from small shallow reef in estuarine area of Bais Bay, Negros Oriental, Central Philippines.

Field identification. This species is relatively easy to identify by its deep uniformly green body and series of pale dots. Pale dots are probably visible at less than 75 mm and remain to at least 315 mm.

Identification notes. In preserved collections, *B. muricatum* is easily distinguished from all other scarids by its deep body, and unusual combination of brown-dark brown body, with scattered dark dots and/or series of pale dots. This species may be distinguished from GBR *Scarus* species as it possesses fewer gill rakers (approx. 20 versus greater than 38 in *Scarus* spp.) and three distinct rows of upper pharyngeal teeth (ratio 3:3:1). The outer row of pharyngeal teeth is greatly reduced or absent in *Scarus* species (ratio approx. 5:2:1).

Previous descriptions. There are few published descriptions of the early juvenile colour patterns of *B. muricatum*. The ontogeny of the colour patterns of relatively small individuals (approx. 200 mm) through to the adult stage are described in Smith (1956). A description of the juvenile phase and a colour plate of a 105 mm specimen from Seribu Island, Java are given in Choat & Randall (1986).

Hipposcarus longiceps (Valenciennes)

Pl. 1D

Material examined. (35 specimens: 29-85 mm). AUSTRALIA - Lizard Island, AMS I. 25783-001 (1:48 mm), AMS I. 25798-001 (1:48 mm); MICRONESIA - Palau, CAS 62579 (3:29-42 mm), CAS 62577 (5:30-67 mm), CAS 62578 (2:30-38 mm), CAS 62576 (3:32-36 mm), CAS 62580 (2:49-59 mm), CAS 62581 (2:40-65 mm), CAS 62582 (1:68 mm), CAS 62594 (15:30-85 mm).

Diagnosis. Median predorsal scales 4, no anterior pair, anterior scale largest; cheek scale rows 3, 2-6 in ventral row, scale rows often indistinct and scales loose; pectoral

rays 15; deep body with distinctly angular snout.

Diagnostic colour notes. Body silver grey to pale tan; caudal fin and caudal peduncle pale yellow; thin beige-orange stripe from snout, through orbit to caudal fin base, terminating with small black dot.

Colour notes. At 48 mm, body silvery grey to pale tan, fading to whitish ventrally, caudal fin and caudal peduncle pale yellow, single thin beige-orange stripe extending from snout, through lower portion of orbit, along flank to caudal fin base, terminating with prominent small black dot (Pl. 1D); stripe particularly striking in field and greatly eases identification; stripe differs from typical orbital stripe of *Scarus* species as passes through lower part of orbit, rather than pupil, and terminates in middle of caudal fin base; caudal fin and caudal peduncle pale yellow, dorsal and anal fins pale tan with off-white mottling and yellow hue medially; in aquaria, 4-5 narrow pale vertical lines may be displayed (faintly visible in Pl. 1D), their locations correspond with pale interspaces of *Scarus* species; colour patterns during transition from juvenile to IP not known, although beige stripe and dark caudal spot lost by 120 mm, leaving uniformly pale body and pale yellow caudal fin closely resembling IP colouration.

Body form. Unusual, body deep with distinctly angular head and snout; body tapers posteriorly to narrow caudal peduncle; dorsal fin appears raised anteriorly.

Colour in alcohol. Body pale brown to brown, pale ventrally, body stripe off yellow to pale brown, terminating with black-brown spot; pale stripe distinct at 29-30 mm, indistinct from 32-67 mm, may be absent greater than 38 mm, usually lost greater than 44 mm; black spot distinct to 42 mm, indistinct to 67 mm, may be absent greater than 53 mm, usually lost greater than 67 mm; vertical fins hyaline to pale brown, dorsal fin darkest, occasionally with faint darker mottling.

Ecology. Rare; solitary, probably site attached; 1 specimen (48 mm) collected over coral rock and rubble, 5 m, Mermaid Cove, Lizard Island; 1 specimen (48mm) over coral rock and boulders at reef slope base (9 m) in semi-exposed site near Crystal Beach, Lizard Island.

In Palau, juveniles collected from rocky shores and near mangroves, 0-13 m, but most abundant in shallow turbid water 0-2 m, in eel-grass beds.

Field identification. Easily distinguished from other GBR scarids by its unusual colour pattern and body shape; care must be taken to distinguish it from *Lethrinus* species (noted below).

Previous descriptions. Masuda *et al.* (1984) figure a 20 mm specimen from the Japanese Archipelago. Choat & Randall (1986) describe the juvenile phase and figure a 38 mm specimen from Papua New Guinea.

Remarks. The body shape and colour pattern of *H. longiceps* more closely resemble those of a *Lethrinus* species rather than those of a *Scarus* species. Some juvenile *Lethrinus* species only differ from *H. longiceps* in the absence of the dark dot at the end of the single medial stripe. The behaviour likewise resembles that of *Lethrinus* species: *H. longiceps* remains motionless above the substratum for extended periods and swims in shorts bursts, periodically feeding on turf algae. It does not school with other scarids and is occasionally aggressive towards them. Overall, its colour pattern and behaviour suggest that it may mimic *Lethrinus* species (Bellwood, 1986).

The unusual features of *H. longiceps* appear to be characteristic of the genus *Hipposcarus*, as the juvenile colour pattern of the Indian Ocean species *H. harid* (Forsskål) (described and figured by Smith, 1959 and described briefly by Randall & Bruce, 1983) is extremely similar to that of juvenile *H. longiceps*.

Scarus altipinnis (Steindachner)

Pl. 4D-G

Material examined. (8 specimens: 20-54 mm). AUSTRALIA - Lizard Island, AMS I.25911-001 (1:20 mm), AMS I.27836-001 (1:24 mm), AMS I.27842-001 (1:25 mm), AMS I.25909-001 (1:28 mm), AMS I.25795-001 (1:29 mm), AMS I.25791-001 (1:52 mm), AMS I.25903-001 (1:54 mm); Yonge Reef, AMS I.25912-007 (1:25 mm).

Diagnosis. Median predorsal scales 6, no anterior pair, scale size decreases anteriorly; cheek scale rows 3, 2-3 in ventral row; pectoral rays 15.

Diagnostic colour notes. Snout yellow orange; less than 30 mm, body and fins with black and white flecks; greater than 30 mm, body grey to brown with white flecks, dorsal, anal and pelvic fins with dark flecks, caudal and caudal peduncle off white.

Colour notes. Distinctive colour pattern, no rapid colour changes; yellow snout and golden-yellow iris visible at 13 mm and persist throughout early juvenile phase; at 12 mm, body off white with 5-7 large black and white flecks approximately equal to orbit, flecks decrease in relative size with growth and at 14 mm are approximately equal to pupil; at 14 mm, white patch similar to that of larger *S. niger* (Pl. 5F) present on caudal fin base; greater than 15 mm (Pl. 4D), white patch fades (remnants visible in Pl. 4D), flecks on body fuse to form broken stripes, dorsal, anal and pelvic fins become mottled; greater than 27 mm (Pl. 4E), caudal fin and caudal peduncle slowly fade to white, body darkens to grey, only few white body flecks or spots remain (although mottled pattern on dorsal and anal fins remains distinct); snout deepens to orange/yellow (Pl. 4F) then to tan; greater than 50 mm, body and fins slowly darken to grey brown; pale body flecks remain, snout darkens to

colour of body (Pl. 4G); during transition to IP, snout, body and fins turn brown, caudal fin and caudal peduncle pale brown, but intensity variable, pale flecks on body remain but of variable intensity; IP colouration complete at approximately 140 mm.

Colour in alcohol. Body pale grey in small specimens, brown in larger specimens; pale snout, caudal fin and caudal peduncle darken but remain distinct; dark body flecks and mottling on fins distinct; white body flecks distinct in large specimens.

Ecology. Uncommon; solitary throughout juvenile phase, often aggressive towards other scarids, especially conspecifics; site attached; settlement sites variable, but usually in spatially complex areas of coral rubble or live coral, from 2-9 m; on Lizard Island, small individuals (12-20 mm) most often recorded at base of reef slope (5-9 m), over coral rock or rubble, larger individuals (20-60 mm) most often recorded near reef crest (2-3 m) or on upper reef slope (3-5 m), in areas of open coral rock and live corals; on Lizard Island and mid-shelf reefs, recorded primarily from moderately exposed reef slopes, occasionally from edge of lagoon patch reefs; on outer reefs, recorded only from backreef bommies.

Field identification. Distinctive colour patterns distinguish this species from all other GBR *Scarus* species. The dark flecks in the dorsal and anal fins are clear throughout most of the juvenile phase and are useful diagnostic features. This is one of the few species that can be identified shortly after settlement by its characteristic yellow snout.

Previous descriptions. The ontogeny of the colour patterns of juvenile *S. altipinnis* were described by Schultz (1958), [as *S. brevifilis* (Günther)]. However, these descriptions were based on preserved material and are therefore of limited use for field identifications. Choat & Randall (1986) briefly describe the late juvenile phase and give a colour plate of a 38 mm specimen from Tongtapo, Tonga and a 47 mm specimen from Tahiti.

Remarks. Choat & Randall (1986) describe *S. altipinnis* as a member of a closely related species complex which comprises *S. altipinnis* in the western, central and southern Pacific, *S. prasiognathos* Valenciennes in the eastern Indian Ocean, Indonesia, Philippines, and north-western Pacific, and *S. falcipinnis* (Playfair) in the western Indian Ocean. The juvenile colour phases of these species are extremely similar, as demonstrated by the published colour plates of *S. falcipinnis* in Randall & Bruce (1983) and of *S. prasiognathos* in Masuda *et al.*, (1984; as juvenile *S. frenatus*). The identity of the latter is based on observations of juvenile *S. prasiognathos* in the Philippines (Bellwood, 1988). However, the restricted geographic ranges of these species minimises potential confusion. Of the three species, only *S. altipinnis* has been recorded from the GBR where it is easily identified.

Scarus bleekeri (de Beaufort)

Pl. 1G,H

Material examined. (5 specimens: 33-60 mm). AUSTRALIA - Lizard Island, AMS I.25916-001 (1:33 mm), AMS I.25903-002 (1:46 mm), AMS I.27815-001 (1:54 mm); Yonge Reef, AMS I.25792-001 (1:60 mm); PHILIPPINES - Sumilon Island, AMS I.27459-002 (1:38 mm).

Diagnosis. Median predorsal scales 4, no anterior pair, anterior 2 scales largest; cheek scale rows 2; pectoral rays 15; based on specimens greater than 33 mm; dental plates exposed in larger specimens.

Diagnostic colour notes. Small individuals with 4 dark brown primary stripes; larger individuals with dark brown body, occasionally with pale vertical bands. All sizes with distinct off-white caudal fin and caudal peduncle.

Colour notes. At less than 25 mm, body off white to grey brown with 4 dark brown-black stripes, medial 2 stripes most distinct, no dorsal division of dorsal stripe, dorsal and anal fins hyaline but darken basally with growth, caudal fin progresses from hyaline to off white; greater than 25 mm, dorsal and ventral stripes slowly fuse with dark bases of dorsal and anal fins, dark orbital and pectoral stripes increasingly pale in caudal peduncle region (Pl. 1G), pale interspaces slowly darken, giving rise to uniformly dark colour pattern, although caudal peduncle and caudal fin remain off white, vertical fins brown at base, hyaline distally; 25-50 mm, intensity of pale interspaces may vary rapidly, resulting in striped or uniformly dark colour patterns; greater than 40 mm, caudal fin and caudal peduncle may also darken resulting in a uniformly dark colour pattern, stripes usually indistinct, caudal fin may have dark distal edge (Pl. 1H). Typical colour pattern of juveniles in field: body and fins uniformly dark-brown black, caudal and caudal peduncle pale off white, but wide range of colour patterns may be displayed (Table 1); greater than 40 mm, this range includes pale vertical bars, a characteristic IP feature, in progressively larger specimens, bars more distinct and displayed more frequently; typical IP colour pattern, with distinctive pale vertical bars and moderately pale caudal fin and caudal peduncle predominates in specimens greater than 110 mm.

Colour in alcohol. Pattern as in live specimens, although dark areas or stripes fade to dark grey and pale interspaces turn pale grey.

Ecology. Uncommon; solitary; site attached; settlement sites unknown; small specimens recorded most frequently in areas of complex coral rubble, 3-9 m, on seaward reef slopes at Lizard Island and backreef bommies of outer barrier reefs; 1 specimen, 3 m, Lizard Island lagoon, over arborescent live coral and soft coral on coral rock; juveniles usually solitary although may occasionally join small multispecies groups; if in areas occupied by adults,

may join 'harems' with individuals ranging from 60-200 mm (=TP).

Field identification. *S. bleekeri* closely resembles *S. sordidus*. Although the two species share a number of colour patterns (Table 1), it can be distinguished from *S. sordidus* and other dark coloured scarids by its pale caudal fin and caudal peduncle.

Scarus chameleon Choat & Randall

Pl. 3C

Material examined. (34 specimens: 9-45 mm). AUSTRALIA - Lizard Island, AMS I.27858-002 (1:23 mm), AMS I.27855-001 to I.27855-005 (5:24-33 mm), AMS I.27831-001 (1:24 mm), AMS I.27833-001 (1:26 mm), AMS I.27840-001 (1:27 mm), AMS I.27830-002 (1:28 mm), AMS I.27837-001 (1:29 mm), AMS I.27832-001 (1:29 mm), AMS I.27832-002 (1:30 mm), AMS I.27856-001 to I.27856-003 (3:30-32 mm), AMS I.25904-001 (3:30-45 mm), AMS I.25799-001 (2:30-43 mm), AMS I.27841-001 (1:31 mm), AMS I.25782-002 (1:32 mm), AMS I.25793-001 (1:33 mm), AMS I.27839-001 (1:34 mm), AMS I.27830-001 (1:35 mm), AMS I.27837-002 (1:38 mm), AMS I.27843-002 (1:41 mm); MacGillivary Reef, Lizard Island, AMS I.27850-001 (1:26 mm), AMS I.27850-003 (1:30 mm), AMS I.27850-002 (1:37mm). Provisional identifications: Lizard Island, AMS 27848-002 (1:9 mm), AMS I.27851-001 (1:11 mm), AMS 27849-009 (1:14 mm).

Diagnosis. Median predorsal scales 4 (occasionally 5), anterior scale moderately large, preceded by a pair of laterally overlapping scales; cheek scale rows 3, 1-3 in ventral row; pectoral rays 14.

Diagnostic colour notes. Snout and/or orbital region of orbital stripe with golden hue, body striped or uniformly brown, pectoral stripe usually terminates at pectoral base; body often with overall golden hue or abruptly pale ventrally; extremely variable colour patterns.

Colour notes. Extremely variable with wide range of colour patterns, able to change patterns rapidly; recently settled specimens (10-14 mm) undergo 'typical' series of colour pattern changes outlined in Fig. 3A-E, body off white, dark stripes pale brown; greater than 15 mm, 2 basic colour patterns predominate: striped or uniform. Striped pattern with 4 basic scarid stripes, body usually off white with pale brown stripes, although whole body often with overall golden hue; striped phase has 3 distinctive features: (1) anterior portion of the orbital stripe frequently golden, golden hue may extend onto opercular portion of stripe, over snout and orbital region, including iris; (2) pectoral stripe typically terminates at pectoral fin base leaving cheek off white; (3) ventral stripe often lost, with ventral region of body being abruptly paler below level of pectoral stripe; less than 40 mm, 2 rows of faint dots may be present in orbital and pectoral stripes, dots clear in newly collected specimens, but often indistinct in field; intensity of striped pattern and frequency of appearance decreases in progressively larger specimens; maximum size at which striped pattern clearly displayed approximately 70-80 mm.

Uniform colour pattern first displayed at approximately 15 mm, becoming increasingly prevalent with increasing size; basic body colour varies from pale tan to dark brown; in shallow water (less than 5 m), body often pale tan with an abruptly off-white belly, in deeper water (greater than 8 m), body often dark brown or mahogany brown; if uniformly dark, iris, snout and orbital region often distinctly golden (golden colouration indistinctly visible in Pl. 3C), alternatively, snout remains pale grey; at 15 mm, fins hyaline, with growth, fins darken, slowly taking on body colour, except caudal fin which may have faint olive-yellow hue greater than 60 mm; 25-45 mm, body may have overall golden hue, which in dark specimens may form reddish colour like burnished copper; 2 series of pale dots along flank visible in dead or captive specimens (Pl. 3C) occasionally apparent in field; golden colour in orbital

Table 1. Variation in the colour patterns of a group of predominantly dark juvenile *Scarus* species.

Species:	bl	gib	so	spi	sch
Uniformly black	+	+	+	+	+
Black, white caudal and caudal peduncle	+				
Black, pale crescent on caudal fin		+			
Black, white caudal peduncle with dark dot			+		
Black, pale vertical bands	+				+
Four dark stripes:	+	+			
- deep black, fins dark basally		+			
- pale caudal and caudal peduncle	+				
Five dark stripes			+	+	
- medial stripes dark or enlarged on caudal peduncle			+	+	
- dorsal stripe with dashed dorsal division			+	+	
- white caudal peduncle with dark dot			+		

Species: bl, *S. bleekeri;* gib, *S. gibbus;* so, *S. sordidus;* spi, *S. spinus;* sch, *S. schlegeli.*

Changes in the colour pattern of a species occur rapidly, usually in less than four seconds and sometimes in less than a second.

region rapidly lost upon capture; dark, random spots on body and fins appear to be cysts or parasite scars, as in *S. psittacus;* characteristic IP colour pattern, with pale yellow caudal fin and brown body, first displayed at about 80mm.

Scarus chameleon can change colour patterns rapidly, especially upon capture; colour patterns described above are based on numerous observations over a range of habitat types; colour pattern appears to correlate with size, location and social behaviour of individuals; in shallow water (less than 5 m), small solitary and schooling specimens tend to be striped, larger specimens uniformly pale; in deeper water (greater than 5 m), all specimens tend to be solitary and uniformly dark.

Colour in alcohol. Colour extremely variable, body uniformly pale or dark, banded, striped or with indistinct dark patches corresponding with regions of overlap of 'typical' scarid bands and stripes, often pale brown with 5-6 pale brown bands on body; orbital and pectoral stripes may be darker at posterior extremities, but not as intensely as in *S. spinus* or *S. sordidus; S. chameleon* retains no characteristic colour pattern.

Ecology. Common; solitary or in small or large (greater than 25 individuals), conspecific or multispecies schools; some individuals site attached when small; settlement sites variable, but include dead coral and coral rubble, 1-9 m, in wide range of habitats including lagoon patch reefs, lower reef slope and rubble covered base of moderately exposed reef slopes; larger juveniles recorded over all substratum types with exception of open sand, from all reef habitats, 1-12 m, most abundant at Lizard Island, on sheltered reef slopes, recorded from reef flat, lagoon and backreef areas of outer shelf reefs; in lagoon and sheltered areas most often observed in small multispecies schools, often with *S. psittacus* and *S. rivulatus*; in deeper water, usually solitary, only occasionally schooling with other species, such as *S. schlegeli* or *S. sordidus.*

Field identification. This is one of the most ubiquitous juvenile scarids. It has a wide range of colour patterns which can change rapidly and is, therefore, one of the most difficult species to identify, particularly as many of the colour patterns are shared with other *Scarus* species. It can be identified when it displays a golden hue restricted to the orbital region, or a truncated pectoral stripe. The abruptly pale belly is also a useful diagnostic feature. However, individuals may have to be followed for several minutes or hours before they display these colour patterns. In shallow water, *S. chameleon* often schools with *S. psittacus* and *S. rivulatus. S. chameleon* is most easily distinguished from these congeners by the abruptly pale ventral region, although it may be necessary to collect specimens for confirmation based on meristic analyses. *S. chameleon* is most difficult to identify in deep water when it has an overall dark hue like that of *S. schlegeli.* It is usually necessary to collect these specimens for meristic analyses. Fortunately, *S. chameleon* can be separated from most other GBR scarids by scale counts.

When recently settled, *S. chameleon* cannot be distinguished from *S. psittacus, S. rivulatus* or *S. schlegeli* in the field; specimens must be reared in aquaria to an identifiable size.

Previous descriptions. A colour description of a 23 mm specimen and a colour plate of a 60 mm specimen from Lizard Island are given in Choat & Randall (1986).

Scarus dimidiatus Bleeker

Pl. 4A

Material examined. (3 specimens: 17-53 mm). AUSTRALIA - Lizard Island, AMS I.25785-002 (1:53 mm); Yonge Reef, AMS I.25912-006 (2:17-30 mm).

Diagnosis. Median predorsal scales 6, no anterior pair, scales subequal; cheek scale rows 3, 2-4 in ventral row; pectoral rays 14.

Diagnostic colour notes. Body yellowish, whitish ventrally, with 5 broad slightly diagonal dark bands on dorsum; bands as wide as pale interspaces and increasingly distinct greater than 20 mm.

Colour notes. A distinctive species, body yellowish to canary yellow, with 5 dark bands on dorsum each as wide as pale interspaces, bands correspond to bands 1-5 of 'typical' scarid banding pattern (Fig. 3), bands faint less than 20 mm and fade in larger specimens when individuals are disturbed; in large specimens (greater than 40 mm), bands 4 and 5 often indistinct; less than 35 mm (Pl. 4A), bands may extend onto lower half of body and onto dorsal fin base, fins hyaline-pale yellow; in larger specimens, bands restricted to dorsum and base of dorsal fin, fins pale yellow; colour patterns of large juveniles (greater than 50 mm) indistinguishable from those of IP individuals; dark medial stripe, often displayed by large juveniles and IPs in central and western Pacific, not noted in juvenile specimens observed on GBR; does not undergo rapid colour changes, with exception of fading of dark bands when stressed or disturbed.

Colour in alcohol. Body yellow green to grey with brown bands; at 17 mm, bands restricted to dorsal part of dorsum near dorsal fin base, fins hyaline; at 30 mm, bands extend faintly onto lower half of body; at 53 mm, bands restricted to upper half of body and along basal part of dorsal fin; fins pale yellow grey.

Ecology. Uncommon; solitary, site attached, rarely joins small multispecies schools; settlement sites probably in live arborescent corals in shallow water (1-5 m); juveniles only recorded in large stands of arborescent coral (primarily *Acropora* spp.; occasionally *Porites cylindrica*), in sheltered, shallow (1-5 m) backreef and lagoonal areas of midshelf reefs, and backreef and reef flat areas of outer

shelf reefs; at Lizard Island, no large juveniles (greater than 80 mm) found in lagoon, may indicate migratory movement as in *S. oviceps*; small individuals (20-25 mm) observed on several occasions in schools of yellow damselfishes (*Pomacentrus molluccensis* and *P. amboinensis*), occasionally feeding within school, possibly on damselfish faecal pellets, as recorded in adult *S. oviceps* by Bailey & Robertson (1982); on GBR, usually solitary, but in areas where they form a dominant part of juvenile scarid populations (e.g. Philippines) will often form small schools with conspecifics or join multispecies schools.

Field identification. The bright yellow body distinguishes this species from all GBR scarid species with the exception of *S. oviceps*. *S. dimidiatus* may be distinguished from the closely related *S. oviceps* by the presence of 4-5 distinct dark bands as wide as the pale interspaces and the lack of a dark orbital stripe on the head.

Remarks. The close relationship between *S. dimidiatus* and the Indian Ocean species, *S. scaber* Valenciennes, and the strong similarity between their IP colour patterns (Randall & Choat, 1980), strongly suggest that the juvenile phase of *S. scaber* will be similar to that of *S. dimidiatus*.

Scarus flavipectoralis Schultz

Pl. 3A,B

Material examined. (4 specimens: 26-45 mm). AUSTRALIA - Lizard Island, AMS I.27858-001 (1:26 mm), AMS I.25782-004 (1:33 mm), AMS I.25787-001 (2: 44-45 mm).

Diagnosis. Median predorsal scales 4, no anterior pair, anterior scale largest; cheek scale rows 3, 1-2 in ventral row; pectoral rays 14; body elongate, spindle shaped.

Diagnostic colour notes. At less than 40 mm, dorsal, orbital and pectoral stripes present, last 2 being darkest; larger specimens with pale body and dark grey caudal fin; pectoral fin pale yellow.

Colour notes. At less than 40 mm, body pale grey tan, prominent dark grey-green orbital and pectoral stripes (Pl. 3A), which may fuse slightly on caudal peduncle, dark dorsal stripe present but often indistinct, belly typically pale, vertical fins pale brown basally, hyaline distally, pectoral fins with faint yellow hue; greater than 40 mm, body pale grey brown, caudal fin dark-grey brown but of variable intensity (e.g. pale in Pl. 3B), dorsal and anal fins pale-grey brown with indistinct mottling, pectoral fins pale yellow; colour patterns change infrequently, most notably in individuals 30-40 mm, which may display either striped or uniformly pale colour patterns; yellow pectoral fin useful diagnostic feature but often exceedingly pale in small specimens; in field, large juveniles typified by elongate pale body and dark caudal fin, closely resembling IP colouration, which is first displayed at approximately 70 mm.

Colour in alcohol. Small specimens (26-33 mm), body pale brown, dark orbital and pectoral stripes retained, dorsal stripe fades; larger specimens (44-45 mm), body pale with dark patches where 'typical' scarid bands and stripes intersect, dorsal, anal and caudal fins pale-grey brown with no distinctive markings.

Ecology. Uncommon; solitary, occasionally joining small multispecies schools; probably site attached; settlement sites unknown; at Lizard Island, juveniles (greater than 26 mm) most frequently recorded over coral rock or rubble at base of reef slope, invariably in deeper water (5-14 m), on both sheltered and exposed reef slopes.

Field identification. This species may be difficult to identify in the field. The most distinctive feature is the elongate spindle-shaped body. The yellow pectoral fins are often too faint to be of diagnostic use. In small specimens, the dominance of the two medial stripes is a useful diagnostic feature, whilst the pale body and dark caudal fin are useful for identifying larger juveniles. However, collection and meristic analyses are recommended, particularly for small specimens.

Scarus forsteni (Bleeker)

Pl. 5H

Material examined. (4 specimens: 49-62 mm). AUSTRALIA - Yonge Reef, AMS I.25908-001 (1:61 mm); PHILIPPINES - Apo Island, AMS I.27461-001 (1:62 mm); Sumilon Island, AMS I.27457-001 (2:49-61 mm).

Diagnosis. Median predorsal scales 5-7, preceded by a pair of laterally overlapping scales; scale size increases posteriorly, third and fourth scales largest; cheek scale rows 3, 2-5 in ventral row; pectoral rays 14; dental plates pale blue-green or off white (see below).

Diagnostic colour notes. At less than 25mm, body off white to pale brown, 4 brown stripes, pale dots in orbital and pectoral stripes; greater than 25 mm, body pale brown, stripes may not be present, single prominent pale dot often present near pectoral fin tip.

Colour notes. A variable species capable of rapid colour changes; smallest specimen observed on GBR 25 mm, colour notes of specimens less than 25 mm based on Philippine specimens; 15-25 mm, body off white with 4 brick red to brown stripes which appear brown in field, 2 rows of pale dots present in orbital and pectoral stripes, corresponding with pale dots in recently settled juveniles (Fig. 3B), dark bar at pectoral fin base not visible; 25-50 mm, contrast decreases between 4 dark stripes and pale interspaces, body and fins take on overall pale brown hue, 2 rows of pale dots in orbital and pectoral stripes slowly fade, lower row first, only 1 dot near pectoral fin tip remains distinct at 50 mm (faint in Pl. 5H); intensity of this pale dot can

change rapidly, but greater than 50 mm becomes increasingly prominent, increasing in relative size; greater than 50 mm, body brown, with pale brown interspaces, anterior region of belly with pale red hue, midbody occasionally with darker slate-blue grey hue, although intensity can vary considerably, often rapidly, dorsal, anal and pelvic fins pale brown (faintly mottled when collected), caudal fin olive-green yellow, pectoral fins hyaline yellow, single dot on body prominent, 2 smaller pale dots may be visible posterior to it; in some individuals, pale dot and dark medial region may be absent, colour pattern therefore uniformly pale brown to brown with faint pale interspaces; greater than 60 mm, pale dot may have a dark bluish patch of variable intensity on its upper border which may extend over pale dot; maximum size at which pale interspaces are displayed approximately 70 mm; IP colour patterns predominate greater than 90 mm; dark bar on pectoral fin base present in freshly collected juveniles greater than 60 mm (Pl. 5H), but not visible in field, dark bar develops shortly after death.

Colour in alcohol. Single 61 mm GBR specimen: body grey, darker dorsally, pale interspaces faintly visible, dark bar at pectoral fin base distinct. Philippine specimens (42-69 mm): body grey brown to brown, palest ventrally, pale interspaces and dots only visible in 62 mm specimen, vertical fins grey brown, dorsal fin darkest; dark pectoral fin base distinct.

Ecology. Rare; settlement sites unknown; solitary specimens (25-70 mm) observed over areas with few live corals and extensive coralline algae, in deep water (9-25 m) on steep outer reef slopes of outer shelf reefs; single specimen observed and collected over coral rock at 5 m, in channel between Yonge and Carter Reefs.

Field identification. The restricted distribution of this species to an area where few other scarid species are found reduces the chances of confusion with other species, whilst the presence of a single pale dot on the side clearly separates this species from all other GBR *Scarus* species. As this pale dot is not always displayed, prolonged observations are often necessary for accurate identifications. The single specimen collected was uniformly brown when first observed and only displayed the pale interspaces and diagnostic pale dot when caught. Small specimens which do not display the diagnostic single pale dot can be distinguished from other species with similar colour patterns (i.e. stripes with pale spots) by the paler body and browner hue, although meristic counts are essential for confirmation.

Previous descriptions. Choat & Randall (1986) describe the late juvenile phase and give a colour plate of a 41 mm specimen from Tutuila, Samoa.

Systematic notes. The single GBR specimen examined in this study has been identified as *S. forsteni* based on its colour patterns, both in the field and when collected, and its meristic values. However, its dental plates were pale blue-green, whereas those of the IP, and of juvenile *S. forsteni* from other geographic locations, are white to off white. Additional observations of this species on the GBR are required, to ascertain if this difference occurs consistently in individuals on the GBR.

There has been some confusion over the identification of this species on the GBR. It was previously identified as *S. tricolor* Bleeker (Randall & Choat, 1980). *S. tricolor* is, however, a closely related species from the Indian Ocean and Western Pacific which has not as yet been recorded from the GBR (Choat & Randall, 1986). The colour patterns of juvenile *S. tricolor* are distinct from those of *S. forsteni* (Bellwood, 1988).

Scarus frenatus Lacepède

Pl. 5B - D

Material examined. (19 specimens 8-95 mm). AUSTRALIA - Lizard Island, AMS I.27860-001 (1:8 mm), AMS I.27863-002 (1:8 mm), AMS I.27862-001 (1:9 mm), AMS I.27862-002 (1:12 mm), AMS I.27840-002 to I.27840-005 (4:9-22 mm), AMS I. 25914-001 (1:10 mm), AMS I.25786-002 (1:19 mm), AMS I.25799-002 (1:28 mm), AMS I.27836-004 (1:31 mm), AMS I.27822-001 (1:95 mm); Yonge Reef, AMS I.27829-001 (1:20 mm), AMS I.25912-002 (2:23-27 mm), AMS I.25912-001 (1:31 mm), AMS I.27820-002 (1:43 mm); North Direction Island, AMS I.25915-001 (1:25 mm).

Diagnosis. Median predorsal scales 6 (rarely 7), scales subequal or decreasing in size anteriorly, often preceded by pair of non-laterally overlapping scales; cheek scale rows 3, 2-4 in ventral row; pectoral rays 14 (rarely 15); based on material greater than 22 mm (median predorsal scales complete at 14 mm; cheek scales complete at 22 mm).

Diagnostic colour notes. At 9-12 mm, yellow green body; 12-24 mm, 3 broad lime green stripes broken by paler dots and irregular pale interspaces; 24-40 mm, body olive green with pale interspaces visible on head, posterior part of body, caudal peduncle and caudal fin pale blue, dorsal and anal fins with red and white flecks; greater than 40 mm, body olive green to pale-red brown (especially in larger individuals), pale interspaces on head give impression of dark longitudinal stripe passing through orbit, caudal fin and caudal peduncle pale blue to off white, dorsal and anal fins with prominent red and white flecks.

Colour notes. A striking species with a series of distinctively coloured stages; changes colour patterns several times during ontogeny, but no rapid colour changes; one of the few scarid species that can be accurately identified when recently settled; 9-12 mm, body pale-yellow green with white dot on caudal fin base, fins hyaline, some specimens may display several series of pale dots (Pl. 5B, cf. Fig. 3A,B); 12-24 mm, pale dots increasingly prominent, overall appearance is of lime green body with

series of pale dots and narrow pale yellow longitudinal lines (Pl. 5C), which are interspaces between 4 broad longitudinal primary stripes, lines give head angular appearance; at approximately 24 mm, white and red flecks first appear at anterior bases of dorsal and anal fins, otherwise fins hyaline.

At 24-40 mm, body slowly changes colour, anterior two thirds of body darkens to olive green, pale interspaces become increasingly faint and restricted to head region where dark orbital stripe may be displayed, posterior third of body fades and takes on pale sky-blue hue, extending onto caudal fin and, in some specimens, onto posterior regions of dorsal and anal fins and along belly (Pl. 5D), pale dots on body become increasingly faint, white and red flecks on dorsal, anal and pelvic fins become more extensive and increasingly distinct.

At greater than 40 mm, overall colour pattern darkens, body darkens to olive brown then red brown, pale interspaces fade, in some specimens pale portions above and below orbit may emphasise a dark orbital stripe extending from snout to operculum, caudal fin and caudal peduncle darken to off white with red-brown hue of variable intensity, flecks in dorsal, anal and pelvic fins deepen before diffusing at onset of IP colouration, otherwise, fins pale red brown; dark scale bases characteristic of IP colouration become increasingly prominent greater than 100 mm; full IP colouration complete at 120 mm.

Colour in alcohol. Small specimens (9-12 mm), body off white to pale yellow, fins hyaline: 12-20 mm, body pale-yellow grey with broad grey-brown stripes, in some specimens 12-15 mm, pectoral stripe wider and darker than other stripes, giving individuals a superficial resemblance to similarly sized *S. rubroviolaceus*; greater than 20 mm, body pale grey brown, pale caudal fin and caudal peduncle indistinct, dark flecks on body and fins retained.

Ecology. Uncommon; solitary, site attached and often aggressive towards other scarids, especially conspecifics, at North Reef, Lizard Island, settled in largest numbers in areas of complex algal-covered coral rubble at base of reef slope (6-8 m); a few specimens settled in lagoon and backreef areas, in areas of structural complexity with extensive growth of turf algae in shallow water (1-3 m); at Lizard Island, small *S. frenatus* observed on numerous occasions, feeding and residing within pomacentrid territories, individuals remained within these territories until approximately 30 mm; most frequently inhabited territories were of *Plectroglyphidodon lacrymatus, Stegastes nigricans, S. apicalis* and *Pomacentrus grammorhynchus*, this relationship does not appear to be obligatory as several specimens also recorded in areas lacking pomacentrid territories; with growth, individual home ranges expanded, and extended up reef slope; at 30 mm, home ranges primarily restricted to reef crest region, including areas within *Acanthurus lineatus* territories, individuals remained in this region throughout remainder of juvenile period, before joining resident harem of adults as IP; a comparable degree of site fidelity was recorded at other locations; at Lizard Island and other midshelf reefs, juveniles recorded from all shallow (1-5 m) reef regions but most abundant in upper reef slope and reef crest; on outer shelf reefs, small specimens only recorded in shallow (1-7 m) backreef areas, few large (greater than 70 mm) specimens recorded from reef slope (5-9 m); detailed notes on biology of juvenile *S. frenatus* given in Bellwood (1986).

Field identification. This is one of the few scarid species that can be accurately identified when recently settled, by its characteristic yellow-green body. At 9-12 mm, *S. frenatus* may be confused with *S. oviceps* and *S. dimidiatus*, and at least one species of labrid (*Halichoeres gymnocephalus*), because of its pale yellow-green colour pattern. The latter can be distinguished in the field by its angular snout and swimming mode, and by meristics if collected. The two other *Scarus* species have not been observed at very small sizes but the smallest specimens examined had a canary-yellow colour rather than the lime-yellow colour of *S. frenatus*. The colour patterns of larger juvenile *S. frenatus* are not shared by any other GBR species. The identification of these later stages is therefore, relatively easy.

Previous descriptions. The colour patterns of moderately large juveniles were described and figured by Schultz (1958), as paratypes of *S. randalli* Schultz. The species description of *S. randalli* was based on the juvenile and IP of *S. frenatus*. A colour plate of a small specimen of *S. frenatus* from the Maldive Islands is given in Randall & Bruce (1983), with a brief colour description. It is interesting to note that this specimen from the Indian Ocean is virtually identical to juveniles of a similar size from the Pacific. The specimen identified as a juvenile *S. frenatus* in Masuda *et al.* (1984; pl. 214H) is probably *S. prasiognathos* (cf. Bellwood,1988). Choat & Randall (1986) give a brief description of the late juvenile phase of *S. frenatus* and a colour plate of a 100 mm specimen from Lizard Island.

Scarus ghobban Forsskål

Pl. 4H

Material examined. (4 specimens: 42-54 mm). AUSTRALIA - Lizard Island, AMS I.27819-001 (1:42 mm), AMS I.25903-003 (1:52 mm), AMS I.27819-002 (1:53 mm), AMS I.27819-003 (1:54 mm).

Diagnosis. Median predorsal scales 6, no anterior pair, scale size decreases anteriorly; cheek scale rows 3, 1 in ventral row; pectoral rays 15.

Diagnostic colour notes. Body pale with yellow hue

and 5 narrow pale blue-white vertical bands, caudal fin dark orange yellow, especially in specimens less than 35mm.

Colour notes. May display several colour patterns, able to change colour patterns rapidly, predominant colour patterns being (a) striped and (b) uniformly pale. Striped pattern: usually displayed by individuals less than 50 mm, dorsal, orbital and pectoral stripes present, stripes tan with orange hue, interspaces similarly coloured but paler, belly off white, vertical bands indistinct, vertical fins with deep orange-yellow hue. Uniformly pale pattern: predominates in individuals greater than 40 mm, body pale tan with orange hue, vertical fins with deep orange-yellow hue, especially caudal fin, 5 narrow vertical bands which correspond with pale interspaces of 'typical' scarid banding pattern (Fig. 4) often distinct; 30-40 mm, bands off white and may vary greatly in intensity, occasionally appearing as 2 rows of pale dots rather than discrete bands; greater than 50 mm, bands clearly visible with blue-white hue.

At greater than 50 mm colour pattern increasingly resembles that of IP, body orange tan to grey yellow, paler ventrally. Freshly collected specimens: belly and pelvic fins with pink hue, pale blue-white vertical bands retained, pectoral fins hyaline, yellow dorsally, medial fins yellow tan, in larger specimens blue markings around mouth and orbit and on cheek become increasingly distinct, blue distal margin of dorsal and anal fins, dorsal and ventral margins of caudal fin and anterior edge of pelvic fins also increasingly distinct; at 80 mm, pale blue dots present along base of dorsal and anal fins, first pectoral spine blue; IP colouration fully developed at about 90 mm.

Colour in alcohol. Body pale brown grey, pale bands visible but faint, some specimens with dark patches corresponding with intersections of 'typical' scarid stripes and bands.

Ecology. Uncommon; most frequently observed in small multispecies schools; settlement sites unknown; at Lizard Island, juveniles (30-90 mm) recorded along edges of extensive reef patches bordered by sand, in shallow (1-3 m) areas of lagoon; on Magnetic Island, an inshore island with fringing reefs, occasionally observed among reef flat sargassum beds, schooling with *S. rivulatus*.

Field identification. When schooling, this species may be initially confused with other schooling species e.g. *S. chameleon*, *S. psittacus* and *S. rivulatus*. However, it may be distinguished by its narrow pale blue-white vertical bands, and by its distinctive deep yellow-orange or golden hue, especially on the fins, which is a deeper colour than that of other schooling species. This is the only GBR scarid with pale vertical bands on a pale body in the field.

Previous descriptions. The late juvenile phase has been described by Choat & Randall (1986) and briefly by Randall & Bruce (1983). Burgess & Axelrod (1974) give a colour plate of an 83.6 mm specimen from Taiwan.

Scarus gibbus Rüppell

Pl. 1E,F

Material examined. (8 specimens: 12-40 mm). AUSTRALIA - Lizard Island, AMS I.25913-001 (2:20-26 mm), AMS I.25909-002 (1:21 mm), AMS I.27836-003 (1:25 mm), AMS I.27825-001 (1:33 mm), AMS I.25782-003 (1:34 mm), AMS I.25905-001 (1:40 mm), AMS I.27843-001 (1:40 mm).

Diagnosis. Median predorsal scales 4, no anterior pair, anterior 2 scales largest; cheek scale rows 3, 3-7 in ventral row; pectoral rays 15-17 (usually 16); based on material greater than 20 mm; dental plates exposed in large specimens.

Diagnostic colour notes. Four black primary stripes, thin in small individuals, relatively wide in large individuals; interspaces white in small individuals, creamy white to yellowish in larger individuals; greater than 20 mm dorsal, anal and caudal fins black.

Colour notes. Dashed phase, 11-13mm (cf. Fig. 3C,D), body bright white with 4 primary rows of black dashes, fins hyaline, dashed orbital and pectoral stripes fuse at about 13-14 mm, followed by fusion of dorsal and anal stripes; with growth, black stripes increase in width and black bases of dorsal, anal and caudal fins slowly expand; at 20 mm, stripes and pale interspaces of approximately equal size (Pl. 1E), black stripes more intense and interspaces whiter than other dark striped juvenile scarids, a series of white dots may be distinct in pale interspaces; greater than 20 mm (Pl. 1F), dark stripes continue to expand and overall appearance is of pale stripes on black background, interspaces creamy yellow to off white, dark fin bases also expand, only edges remain hyaline, pectoral fin yellow proximally, hyaline distally; greater than 40 mm, pale interspaces darken, resulting in uniformly black pattern, although faint pale interspaces may be displayed occasionally, yellow hue of pectoral fins distinct; uniformly dark pattern maintained to approximately 80 mm when pale crescent may be displayed on caudal fin; greater than 80 mm, body and fins slowly fade and take on green hue, blue-green markings increasingly prominent around mouth, on distal borders of median fins and on caudal fin, especially along longest dorsal and ventral rays, diagnostic pale green bar across cheek develops subsequently; IP colour pattern complete at about 150 mm; deep body and blunt profile with sloping forehead noticeable at this size.

Colour in alcohol. Patterns as in live specimens, but black stripes and fins become dark grey, pale interspaces become pale grey. Uniformly dark specimens remain uniformly dark grey.

Ecology. Moderately common; site attached; recently settled individuals most frequently observed amongst large algal covered arborescent coral fragments at reef slope base (7-10 m); no specimens observed in pomacentrid

territories; juveniles recorded most often over coral rock or large coral rubble fragments, in deep water (4-12 m), most frequently on, or at base of, reef slope, in exposed and semi-exposed locations of mid shelf reefs and backreef bommies of outer shelf reefs; 1 or 2 individuals observed in lagoon and on reef crest at Lizard Island; small individuals may join small multispecies groups comprising 3-5 individuals, but greater than 30 mm invariably solitary.

Field identification. Small *S. gibbus* are easily distinguished from other dark juvenile scarids (Table 1) by the intense black and white stripes and black caudal fin base. In the uniformly dark black phase, it may be separated from *S. spinus* and *S. schlegeli* by its head shape, but cannot be distinguished from *S. bleekeri* or *S. sordidus* until the latter display their diagnostic colour patterns, or if the pale caudal crescent and pale yellow pectoral fins of *S. gibbus* are visible. Small *S. gibbus* (less than 30 mm) may initially be confused with juvenile *Labropsis australis* which have a similar colour pattern (described by Randall, 1981). *L. australis* may, however, be distinguished from *S. gibbus* by its more angular profile, elongate body, and distinctive exaggerated sinuous swimming motion. *S. gibbus* does not undergo rapid colour changes. The most variable stage is towards the end of the uniformly black phase, when it may display no pale markings, faint longitudinal stripes, or the pale crescent in the caudal fin. These changes are relatively slow and do not follow any distinct behavioural patterns.

The juvenile colour patterns of the red phase of *S. gibbus* (*sensu* Randall & Choat, 1980) are unknown. No juvenile specimens attributable to this colour morph were observed, although it is likely that the two GBR phases of *S. gibbus* share a common juvenile colour pattern.

Previous descriptions. The late juvenile stage of *S. gibbus* has been described briefly by Schultz (1958; as *S. microrhinos* Bleeker), Randall & Choat (1980), Randall & Bruce (1983; with a colour plate of a 59 mm specimen), and Choat & Randall (1986; with colour plates of a 59 mm and a 65 mm specimen). Burgess & Axelrod (1973b, p. 631, pl. 89) provide a colour plate of a juvenile scarid from the Maldives (as *Scarus* sp.). This specimen is indistinguishable from juvenile *S. gibbus* from the Pacific.

Scarus globiceps Valenciennes

Material examined. (5 specimens: 25-59 mm). AUSTRALIA - Lizard Island, provisional identifications, AMS I.27852-001 (1:22 mm), AMS I.27839-004 (1:25 mm), AMS I.25910-002 (1:25 mm), AMS I.27847-001 (1:29 mm), AMS I.25797-001 (1:59 mm).

Diagnosis. Median predorsal scales 5-6, often laterally overlapping anterior pair, scale size reduced anteriorly; cheek scale rows 3, 3 in ventral row; pectoral rays 14; based on selected specimens, see below.

Diagnostic colour notes. A variable species, extremely similar to *S. rivulatus*. *S. globiceps* has no discernable unique or diagnostic colour patterns.

Colour notes. Specimens provisionally identified as *S. globiceps* displayed 2 basic colour patterns: striped or uniformly pale. Striped phase: body pale tan with 4 dark tan-brown primary stripes; in small specimens (less than 25 mm), caudal extremities of medial stripes may be darkened, similar to, but not as intense as in *S. sordidus* and *S. spinus*. Uniformly pale colour pattern: body pale tan grey, fins pale grey, most often seen in large individuals, appear slightly darker grey brown than *S. rivulatus;* overall, colour patterns closely resemble those of *S. rivulatus*.

Colour in alcohol. Specimens provisionally identified as *S. globiceps* were uniformly grey brown, with darker dorsal surface; one specimen had faint body stripes, and dashes at base of dorsal and anal fins.

Ecology. Individuals tentatively identified as *S. globiceps* observed in small multispecies schools, over sand and coral rubble, in shallow water (1-4 m), in reef flat, backreef and lagoonal areas of Lizard Island; adults abundant on mid- and outer shelf reefs but rare or absent from inshore reefs (Russ, 1984; Williams, 1982), juveniles therefore most likely to be observed in first two localities.

Field identification. Juvenile *S. globiceps* are extremely difficult to identify both in the field and in preserved collections because of their similarity to juvenile *S. rivulatus*. Mature IP specimens of both species often have extremely similar colour patterns but can be separated, when collected, by their meristic values and

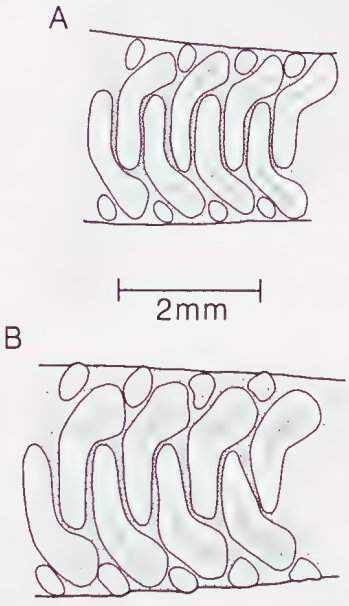


Fig.6. A ventral view of the upper pharyngeal tooth rows of (A) *S. globiceps* and (B) *S. rivulatus*. Both figures are of the midregion of the upper pharyngeal bones, posterior to the first worn tooth. Both specimens were 128 mm SL.

caudal fin shape. The validity of these factors have been confirmed by analyses of the sexual status of individuals in mixed collections, as *S. globiceps* matures at a smaller size than *S. rivulatus* (Randall & Choat, 1980). Unfortunately, there is some degree of overlap between the two species in their scale counts, and less than 130 mm the caudal fin shape is not a useful diagnostic character (Randall & Choat, 1980).

In this study, therefore, specimens were provisionally identified as *S. globiceps* if they: (a) consistently maintained *S. rivulatus*-like colour patterns, especially the striped and uniformly pale phases, but did not show any signs of a yellow caudal fin or caudal peduncle, and (b) had six or fewer median predorsal scales and three or more scales in the ventral cheek scale row (Randall & Choat, 1980).

Morphological notes. The form of the upper pharyngeal tooth plates of mature IP *S. globiceps* and *S. rivulatus* are consistently different. In *S. globiceps*, the dental plate is relatively small and elongate, with strongly interdigitating medial tooth rows, forming a rhabdom-like central region (Fig. 6A). In contrast, *S. rivulatus* has a more robust dental plate, larger, rounded teeth and less strongly interdigitating medial tooth rows (Fig. 6B). These differences were consistent in specimens greater than 114 mm and may assist in the identification of *S. globiceps* and *S. rivulatus* as juveniles.

Scarus longipinnis Randall & Choat

Pl. 3D,E

Material examined. (2 specimens: 39-75 mm). AUSTRALIA - Lizard Island, AMS I.25789-001 (1:39 mm); Carter Reef, AMS I.25784-001 (1:75 mm).

Diagnosis. Median predorsal scales 4, no anterior pair, anterior scale largest; cheek scale rows 3, 1-3 (usually 2) in ventral row; pectoral rays 14; relatively long dorsal spines and rays distinguishable at 75 mm.

Diagnostic colour notes. Small individual (39 mm), body pale tan with 7 dark brown vertical bands; larger individual (75 mm), body uniformly pale mahogany brown (banding variable); both sizes with distinct dark spot on dorsal fin base between first 2 spines and dark crescent-shaped patch on middle of caudal fin.

Colour notes. Rapid colour pattern changes not observed; at 39 mm (Pl. 3D), body off white, with 7 dark brown bands extending onto dorsal and anal fin bases, dorsal fin pale brown, with distinct dark basal spot between first 2 spines, pectoral fins and distal ends of pelvic and anal fins hyaline, caudal fin pale brown with dark medial patch (indistinct in Pl. 3D); pale body and dark brown bands particularly distinctive in field; at 75 mm (Pl. 3E), body deep mahogany brown, 2 pale blue stripes extend from mouth to orbit, 1 across cheek, 3 along belly, dorsal and anal fins olive brown, anal edged with broad blue band, dark spot between first 2 dorsal spines still distinct, pelvic fins red brown at base, pale blue hue distally, caudal fin with orange dorsal and anal margin and distinct dark medial patch, characteristic elevated dorsal fin apparent at this size.

Colour in alcohol. At 39 mm, body pale brown grey, dark bands visible but faded except where orbital and pectoral stripes would pass, giving the appearance of 2 diffused dashed lines, fins brown hyaline; pattern similar to preserved colour pattern of some specimens of *S. chameleon* and *S. ghobban;* at 75 mm, body uniformly dark grey brown, fins slightly paler; in both specimens, small dorsal spot and dark caudal patch retained.

Ecology. Rare in Lizard Island and central GBR regions; 39 mm specimen collected over algal-covered coral rubble at 4 m, Mermaid Cove, Lizard Island, in multispecies school including *S. chameleon, S. psittacus* and/or *S. schlegeli;* 75 mm specimen collected between large coral boulders on sand, 9 m, at base of backreef coral bommie on Carter Reef, with small group of juvenile scarids when first observed but subsequently remained solitary. Adults rare in northern GBR where it is typically found in deeper portions (20-30 m) of outer reef fronts; more abundant in shallower water (10-15 m) in southern GBR and is reported to be most abundant scarid species on Coral Sea reefs (Choat & Randall, 1986).

Field identification. Although large juveniles may be confused with other dark bodied species, the banded phase is easily distinguished as no other GBR *Scarus* species displays dark bands on a pale body. The most distinctive characteristic of larger specimens is the dark caudal patch combined with the dark body. Once collected, the dark spot on the dorsal fin is also diagnostic, although this spot is present (but faint) in several other *Scarus* species, including *S. chameleon* and *S. globiceps*.

Previous descriptions. Randall & Choat (1980) describe a 35 mm paratype as "...pale with exceedingly faint bars as in adults".

Scarus niger Forsskål

Pl. 5E-G

Material examined. (32 specimens: 8-57 mm). AUSTRALIA - Lizard Island, AMS I.27863-001 (1:8 mm), AMS I.25914-002 (2:8-9 mm), AMS I.27862-003 to I.27862-005 (3:8-10 mm), AMS I.27863-003 (1:9 mm), AMS I.27860-002 (1:9 mm), AMS I.27857-001 (1:12 mm), AMS I.27836-005 to I.27836-009 (5:17-31 mm), AMS I.25909-004 (4:19-22 mm), AMS I.27828-002 (1:20 mm); Yonge Reef, AMS I.27829-002 to I.27829-006 (5:15-24 mm), AMS I.25912-004 (2:20-23 mm), AMS I.25907-001 (1:57 mm); PHILIPPINES - Apo Island, AMS I. 27808-001 to I.27808-004 (3:17-45 mm); Sumilon Island, AMS I. 27809-001 (1:55 mm), AMS I.27460-001 (1:55 mm).

Diagnosis. Median predorsal scales 7 (occasionally 6), usually no anterior pair (occasionally non-laterally overlapping pair), scales subequal or reduced anteriorly; cheek scale rows 3, 3-4 in ventral row; pectoral rays 14; based on specimens greater than 20 mm, smaller specimens have lower cheek scale counts; median predorsal scales complete at 13 mm; large individuals with pale blue-green dental plates.

Diagnostic colour notes. At less than 10 mm, lower half of body dark, upper half translucent, body with series of white pupil-sized dots; 10-40 mm, lower portion of body dark with numerous small pale dots, upper part mottled olive green, white patch on caudal fin base preceded by 2 dark spots; 25-40 mm, caudal peduncle burgundy red; greater than 40 mm, body dark brown black, darkest ventrally, small pale dots on body faded, caudal peduncle pale red brown to brown, white patch at caudal fin base diffused and dark dots faded.

Colour notes. No rapid colour changes; at less than 9 mm, recently settled individuals with characteristic row of dark patches along ventral surface, dorsum remains transparent; 9-10 mm (Pl. 5E), lower half of body dark, upper half translucent, distinctive white dot present on caudal fin base, series of white pupil-sized dots on body correspond to 'typical' juvenile scarid pattern (Fig. 3A,B), fins hyaline.

At greater than 10 mm (Pl. 5F), dorsum mottled olive green, in progressively larger specimens, dark colouration in ventral part of body extends dorsally onto flank, and ventrally onto ventral and pelvic fins, olive colouration on dorsum extends onto dorsal fin, pale dots on body decrease in relative size, although increasing in number, dots may be white or pale blue and may be arranged in horizontal rows corresponding with scale rows (Pl. 5F), not with pale interspaces of 'typical' scarid pattern (Figs 3E, 4), caudal fin hyaline with bright white hemispherical patch at base, preceded by 2 black dots at bases of most dorsal and ventral caudal fin rays, ventral dot first visible at approximately 15 mm, dorsal dot at 20 mm, both dots increase in relative size in progressively larger specimens, pectoral fins hyaline to pale yellow; 25-40 mm caudal peduncle often deep burgundy (Pl. 5F), slowly fading to red then red brown at about 50 mm.

At greater than 50 mm (Pl. 5G), body gradually darkens to deep brown black, fins to dark brown, pale dots on body gradually lost, white patch on caudal fin base diffuses, then darkens, 2 dark caudal dots fade, pale yellow pectoral fin conspicuous from 50-65 mm but loses intensity and darkens in larger specimens; greater than 80 mm, green lines around mouth and under orbit, and blue-green margins on dorsal, anal and caudal fins become increasingly distinct; IP colouration first displayed at about 90 mm.

Colour in alcohol. Distinctive colour pattern retained and closely resembles that of live specimens, body remains dark-brown black ventrally, olive green to pale brown dorsally; this contrast decreases in larger specimens, which often have an overall dark grey-brown body; 2 dark spots on caudal fin base remain distinct, white caudal patch usually indistinct, pale body spots visible in small specimens but extremely faint in larger specimens.

Ecology. Moderately common; solitary, site attached, occasionally joining small multispecies schools; settlement sites in areas of complex algal covered coral rock or rubble, in deep water 4-10 m, typically at base of semi-exposed reef slopes or backreef bommies; with growth, home ranges of individuals expand and occupy most of reef slope region from 1-12 m, with exception of precipitous dropoffs which are often devoid of juvenile scarids; all individuals remain close to cover, although larger individuals may occasionally feed in areas of open rock or rubble; juveniles most abundant in deeper water (4-8 m) in relatively sheltered areas, typically over coral rock or rubble, on and at base of reef slopes, from 2-12 m; recorded from reef slope, lagoon and backreef areas of Lizard Island and other midshelf reefs, and backreef areas of outer shelf reefs; although usually solitary, may join small multispecies schools when small; larger specimens often aggressive to similar-sized conspecifics; such antagonism ceases at dusk, some large juveniles gather in small conspecific groups at base of reef slope, near to nocturnal resting sites, in or amongst large coral rubble fragments.

Field identification. *S. niger* is one of the few species that can be accurately identified shortly after settlement. It is easily distinguished throughout its juvenile phase from all other GBR scarid species by its unique colour patterns. Individuals are often difficult to locate in the field because of their cryptic colouration. From above, the mottled olive dorsum blends with the algal covered substratum, whilst from the side, the dark body matches the numerous small holes or overhangs in the areas in which this species is typically found.

Previous descriptions. The colour pattern of late juvenile phase *S. niger* has been described briefly by Schultz (1958), Randall & Bruce (1983) and Choat & Randall (1986). Randall & Bruce (1983) included a colour plate of a 45 mm specimen from the Society Islands. Choat & Randall (1986) provide a colour plate of a 45 mm specimen from Tahiti and a 50 mm specimen from Lizard Island.

Remarks. An aquarium specimen (approximately 60 mm) of unknown origin photographed by R. Kuiter was superficially similar to the *S. niger* examined but differed in several important aspects. As in the *S. niger* examined from the GBR (and the Philippines): body black, olive dorsally; cheek, anterior belly and caudal fin reddish, the latter preceded by a pair of dark dots; mouth bordered by two green lines. This specimen differed from GBR specimens in that it possessed: blue vermiculations on the rear of the head; red-brown dorsal and anal fins with a blue basal stripe; a series of seven longitudinal rows of small blue dashes on the body, and lacked a white patch at the base of the caudal fin. This specimen bears a strong resemblance to the IP of the Indian Ocean colour morph of *S. niger*,

previously known as *S. madagascarensis* (Steindachner) described by Smith (1956), Schultz (1958, 1969) and Randall & Bruce (1983). As the geographic source of the specimen is unknown, it remains to be established whether the specimen represents the Indian Ocean morph of *S. niger,* an anomalous GBR form, or the undescribed juvenile phase of another species.

A colour plate of juvenile scarid from Mombassa provided by Burgess & Axelrod (1973b, p. 630, pl. 87) probably represents the late juvenile stage of the Indian Ocean morph of *S. niger.* As in the specimen described above, it possesses a series of blue dashes on the body. Two characteristic features of juvenile *S. niger,* i.e. dark dots at the base of the caudal fin and dark bands around the mouth, are visible but exceedingly faint.

Juvenile *S. niger* observed and collected in the Central Visayas, Philippines were indistinguishable from GBR specimens.

Scarus oviceps Valenciennes

Pl. 4B,C

Material examined. (4 specimens: 32-73 mm). AUSTRALIA - Lizard Island, AMS I.25794-002 (1: 32 mm), AMS I.25794-001 (1:73 mm); PHILIPPINES - Sumilon Island, AMS I.27459-001 (2:54-55 mm).

Diagnosis. Median predorsal scales 6, no anterior pair, scales subequal; cheek scale rows 3, 2-3 (usually 3) in ventral row; pectoral rays 14.

Diagnostic colour notes. Body yellow, whitish ventrally, with dark orbital stripe from snout to opercular edge, a dark area dorsal to this stripe extends to anterior rays of dorsal fin, four slightly diagonal dark bands on dorsum often indistinct, bands wider than interspaces.

Colour notes. Body pale to bright yellow, whitish ventrally, short dark grey orbital stripe extending from snout, through orbit, to slightly beyond posterior edge of operculum, grey region dorsal to orbital stripe extending to anterior rays of dorsal fin and include upper half of band 1 of 'typical' scarid pattern (Fig. 4B); 4 short dark grey diagonal bands may be present on dorsum, corresponding to bands 2-5 of 'typical' scarid pattern, dark bands wider than pale interspaces, often indistinct, especially bands 4 and 5, and may extend onto dorsal fin base, fins hyaline yellow at 25 mm, yellow in larger specimens, short orbital stripe and dark dorsal region present in all specimens observed (all greater than 25 mm) but faint in newly caught small specimens; colour pattern of individuals greater than 50 mm closely resembles that of IP.

Colour in alcohol. Body yellow green to brown, paler ventrally, with distinct dark brown bands; bands extend onto belly at 32 mm, but restricted to dorsum greater than 54 mm; distinctive short dark orbital stripe retained in all specimens.

Ecology. Uncommon; solitary; site attached; settlement sites unknown; juveniles only recorded amongst live corals, in areas with abundant live coral, particularly arborescent *Acropora* species, in shallow water (1-5 m), from reef flat, backreef and lagoon of mid- and outer shelf reefs; often recorded in same location as *S. dimidiatus;* several large juvenile *S. oviceps* recorded in lagoon at Lizard Island, but no specimens greater than 85 mm observed during 25 month study period; absence of larger individuals may indicate migratory movement during late juvenile stage as in *S. sordidus.*

Field identification. The short dark orbital stripe and the dark area dorsal to this stripe distinguish this species from the closely related *S. dimidiatus.* The dark bands of *S. oviceps* are broader and more oblique than those of *S. dimidiatus.*

Previous descriptions. A description of the late juvenile phase and a colour plate of a 95 mm specimen from Tongtapu, Tonga are given in Choat & Randall (1986).

Scarus psittacus Forsskål

Pl. 2F

Material examined. (20 specimens: 23-49 mm). AUSTRALIA - Lizard Island, AMS I.27834-001 (1: 23 mm), AMS I.27859-001 to I.27859-0011 (11: 25-44 mm), AMS I.27823-005 to I.27823-007 (3: 26-49 mm), AMS I.25917-001 (1:28 mm), AMS I.27824-001 (1:32 mm), AMS I.25782-005 (1:34 mm), AMS I.27817-003 (1:37 mm), AMS I.27835-001 (1: 38 mm).

Diagnosis. Median predorsal scales 4, no anterior pair, anterior scale largest; cheek scale rows 2; pectoral rays 14.

Diagnostic colour notes. Extremely variable, typically uniformly pale grey-tan or striped, belly pale; body often with distinct dark dots (cysts). Striped pattern with 4 pale grey-brown primary stripes; orbital stripe relatively wide, ventral stripe indistinct, interspaces pale grey-tan; some small specimens with pale brown stripes and bronze interspaces.

Colour notes. Extremely variable, capable of rapid colour pattern changes; recently settled individuals (9-15 mm) follow 'typical' sequence of colour pattern changes outlined in Fig. 3, body off white, 'dark' stripes pale brown; as in other species, rapid colour pattern changes only observed in individuals with complete striped colour pattern, i.e. greater than 15 mm.

At greater than 15 mm, 2 dominant colour patterns displayed, striped or uniformly pale. Striped pattern: body pale tan-grey with grey-brown dorsal, orbital and pectoral stripes, ventral stripe usually indistinct, orbital stripe relatively broad and may fuse with pectoral stripe on caudal peduncle; in some small individuals less than 25 mm, dark

stripes grey brown, interspaces metallic bronze, row of 4-6 small bronze dots within dark stripes. Overall hue may vary from dark grey-tan to extremely pale grey or tan; larger individuals (25-50 mm), stripes dark-grey brown, interspaces pale brown, a relatively dark grey orbital stripe is characteristic of this species at 25-50 mm (indistinctly visible in Pl. 2F).

Uniformly pale pattern: displayed by individuals greater than 20 mm, but most frequently greater than 40 mm; characterised by uniformly pale body and fins, colour may vary from extremely pale grey or tan to pale brown, darker specimens typically with pale snout, most common colour is pale grey-tan; greater than 40 mm, pelvic fins with pale red hue; greater than 60 mm, body and medial fins pale grey-tan to pale brown, snout slightly paler than body, pelvic fins pale red; colour pattern at 60 mm closely resembles that of IP.

Colour in alcohol. Body uniformly pale brown, occasionally with darker patches where 'typical' scarid bands and stripes intersect, fins pale brown to off white, occasionally with exceedingly faint dashes at base of dorsal and anal fins; because of overlap in colour patterns of preserved specimens of *S. psittacus* and *S. schlegeli,* and apparent lack of meristic differences, some preserved specimens can only be identified as *S. psittacus/schlegeli.*

Ecology. Common; schooling; may be site attached up to 40 mm; recently settled individuals recorded from algal-covered coral rock and rubble, in shallow (1-3 m) sandy coral rubble areas, in lagoon and backreef areas of Lizard Island; juveniles most frequently recorded over sand and coral rubble or rock, in shallow (1-5 m) sheltered areas, including reef flat, backreef and lagoon; one of most abundant species in shallow water on mid-shelf reefs, usually in small (approximately 5 individuals) to large (greater than 25 individuals) conspecific or multispecies schools.

Field identification. *S. psittacus* often schools with other pale juvenile *Scarus* species, including *S. rivulatus* and *S. chameleon.* When uniformly pale, *S. psittacus* can most easily be distinguished from these species by its paler colour, the lack of an abruptly pale belly, and frequently by the possession of small (1-1.5 mm) dark round cysts on the body and fins. Similar cysts were only occasionally observed on other species, primarily on *S. chameleon.* In the striped phase, *S. psittacus* may be distinguished by its relatively broad, dark orbital stripe. However, collection and meristic analyses are recommended to check field identifications. Recently settled and other small specimens cannot be distinguished from similar pale species with any degree of accuracy.

Uniformly dark specimens of *S. psittacus* are difficult to distinguish from *S. schlegeli.* The differences between these species in the field are discussed under the 'Field Identification' section of *S. schlegeli.*

Positive identifications of *S. psittacus* were restricted to specimens exhibiting diagnostic colour patterns in the field. Small specimens were maintained in aquaria until greater than 25 mm when meristic values could be taken.

Previous descriptions. Choat & Randall (1986) briefly describe the late juvenile phase and provide colour plates of two specimens, 43 mm and 50 mm, from Enewetak, Marshall Islands.

Scarus rivulatus Valenciennes

Pl. 5A

Material examined. (8 specimens: 36-54 mm). AUSTRALIA - Lizard Island, AMS I.27823-009 (1: 36 mm), AMS I.27823-008 (1:41 mm), AMS I.27819-002 (1:42 mm), AMS I.27817-001 (1:47 mm), AMS I.25788-001 (1:49 mm), AMS I.25796-001 (1:50 mm), AMS I.27819-001 (1:50 mm), AMS I.27817-002 (1:54 mm).

Diagnosis. Median predorsal scales 5-6 (usually 6), occasionally with laterally overlapping anterior pair, scales subequal or smaller anteriorly; cheek scale rows 3, 2 (rarely 3) in ventral row; pectoral rays 14.

Diagnostic colour notes. A variable species, body typically pale tan or olive tan; caudal fin and caudal peduncle with yellow hue which may extend onto midbody.

Colour notes. Small juveniles (less than 17 mm), body off white with grey to grey-tan dorsal, orbital and pectoral stripes, belly off white. Striped pattern, with grey-tan stripes and pale grey-tan interspaces, often displayed less than 25 mm, but may be displayed to 60 mm, most often by solitary individuals or individuals in conspecific schools on inshore reefs, predominating in captivity (to 55 mm). In field, most juveniles (greater than 20 mm) body, dorsal and anal fins uniformly pale olive-tan, pectoral fins hyaline, caudal fin and caudal peduncle usually with pale yellow hue which may extend onto posterior flank; occasionally body may have overall pale yellow or golden-yellow hue, usually in individuals among sargassum beds on inshore reefs; greater than 55 mm, body may assume darker shade, with dark scale edges, losing yellow hue on body and caudal fin (as in Pl. 5A), dorsal margin of sclera often distinctly pale blue, this colour pattern characteristic of recently collected specimens as yellow hue quickly lost upon capture, also recorded in larger specimens in schools, especially near dusk.

Colour in alcohol. Body tan, grey or grey brown, darker dorsally; some specimens with faint dashes at base of dorsal and anal fins and on body where 'typical' scarid pattern of bands and stripes intersect; other specimens, with dark patch on middle of each scale.

Ecology. Common; occasionally solitary, usually in small (approx. 5 individuals) to large (greater than 25 individuals) conspecific or multispecies schools; site attached when small; at Lizard Island, recently settled individuals observed on few occasions in areas of live hard

and soft coral and coral rubble, in shallow water (2-3 m), along edges of large lagoon patch reefs; at Lizard Island and other midshelf reefs, juveniles recorded over all substratum types except open sand, in shallow water (1-6 m), including reef flat, lagoon and other sheltered areas; some small individuals (less than 45 mm) in regions of high coral cover may be solitary with small home ranges and may be aggressive to other *Scarus* species; greater than 45 mm, most individuals join schools and move off over open areas to feed, these individuals are highly mobile, having either large home ranges or seminomadic behaviour; on inshore reefs, juveniles most abundant on reef flat, especially in sargassum beds; in most inshore localities, it is the only *Scarus* species present, often forming relatively large conspecific schools.

Field identification. This is a variable species capable of rapid colour pattern changes. It shares several colour patterns with other species, including *S. chameleon, S. globiceps* and *S. psittacus. S. rivulatus* often schools with *S. psittacus, S. chameleon* and probably *S. globiceps.* It can be easily distinguished from the first two species which are typically paler, especially ventrally, and have more elongate bodies. At Lizard Island, *S. rivulatus* has two predominant colour patterns: (a) a pale olive-tan body with darker scale edges (as in Pl. 5A), and (b) a pale olive-tan body with a pale yellow or golden-yellow caudal fin and caudal peduncle. The first pattern distinguishes *S. rivulatus* from all other GBR species with the exception of *S. globiceps.* The second pattern distinguishes it from all GBR scarid species including *S. globiceps.* At Lizard Island, this unique pattern is retained in the IP and aids in the identification of IP *S. rivulatus.* However, this pattern may not be retained or possessed by *S. rivulatus* in other GBR localities (Randall & Choat, 1980). See the species description of *S. globiceps* for notes on its similarity to *S. rivulatus,* and a possible means of separating the two species.

Scarus rubroviolaceus Bleeker

Pl. 3F-H

Material examined. (7 specimens: 12-38 mm). AUSTRALIA - Lizard Island, AMS I.25790-001 (4: 12-18 mm), AMS I.27845-001 (1:17 mm), AMS I.25909-003 (1:22 mm), AMS I.25902-001 (1:38 mm).

Diagnosis. Median predorsal scales 6, no anterior pair, 2 anterior scales smallest, remainder subequal; cheek scale rows 3, 2 in ventral row; pectoral rays 15.

Diagnostic colour notes. At less than 25 mm, body off white, 3 brown stripes, orbital and dorsal stripes faint, pectoral stripe broad and dark, especially posteriorly; greater than 25 mm, stripes olive green, dorsal and orbital stripes increasingly visible, pale dots clearly visible in orbital and pectoral stripes, single broad dark vertical band extending from dorsal spines 3-8 distinct in small individuals but fades in progressively larger specimens; greater than 40 mm, body pale brown, scales with dark posterior margins, pale dots and interspaces become increasingly faint.

Colour notes. A relatively distinctive species, no rapid colour changes, can be identified when recently settled; recently settled individuals (less than 10 mm), body off white, with 3 dashed brown lines, fins hyaline, pectoral line notably wider than dorsal and orbital lines, and fuses first; 10-12 mm, pectoral line appears as a broad stripe with pale dots interspersed along its length.

At 14-25 mm (Pl. 3F,G), body off white, some scales with darker red-brown patches, dorsal, orbital and pectoral stripes olive green, orbital and dorsal lines fuse to form stripes at about 25 mm, dorsal stripe lies close to base of dorsal fin, but leaves short, pale interspace along midline anterior to dorsal fin, snout may have pale green hue, 2 series of pale white dots on body and pale patch at caudal fin base, as in 'typical' juvenile scarid pattern (Fig. 3), retained, iris pale olive green, brown and white flecks on base of dorsal, anal and pelvic fins, otherwise fins hyaline; dark brown-olive green vertical band corresponding to band 2 of 'typical' scarid pattern (Fig. 4) first displayed at about 14 mm, band extends from dorsal spine 3-8 and is darker dorsally (Pl. 3G), band may be faint in specimens less than 25 mm, if so, dashes or part of stripes in region of band darker than remaining dashes or striped regions (Pl. 3F).

At 25-40 mm (Pl. 3H), dorsal, orbital and pectoral stripes clearly visible, brown and white flecks still restricted to fin bases, iris olive brown, pale dots on body retained and clearly visible in orbital and pectoral stripes, particularly posteriorly, dark vertical band fades in progressively larger specimens and lost at about 40 mm, scale edges start to darken at about 38 mm, dark pectoral base visible in Pl. 3H not visible in live specimens; greater than 40 mm, stripes fade, starting with pectoral stripe anterior to pectoral fin base, pale dots of variable intensity, body takes on more uniform brown hue and dark scale edges become increasingly prominent.

At 80 mm, body pale brown-grey with dark scale edges, pale interspaces and pale dots faintly visible or lost; IP colouration almost complete by 150 mm, although typical IP colour pattern, ie. with abruptly darker anterior half, not displayed by specimens less than 200 mm at Lizard Island or on nearby outershelf reefs.

Colour in alcohol. Colour pattern closely resembles live specimens: body pale grey with distinct dark grey brown dashes, with or without stripes, pale dots in orbital and pectoral stripes retained, pectoral fin base dark but not as intense as in *S. forsteni;* smaller specimens (14-22 mm), dark vertical bar retained but faint.

Ecology. Uncommon; solitary, occasionally joining small multispecies schools; site attached; settlement sites variable; several recently settled juveniles collected from algal 'lawns' within pomacentrid (*Dischistodus* spp.)

territories at reef slope base, North Reef, Lizard Island, other specimens from patches of algal-covered coral rubble near reef slope base (6-9 m); small juveniles (12-15 mm), recorded from upper reef slope regions on several occasions although recently settled individuals only observed below 6 m; larger juveniles (20-50 mm), observed over open coral rock or rubble, occasionally among stands of arborescent live corals, in areas extending from reef crest (1-2 m) to reef slope base (8-12 m); individuals greater than 50 mm most often observed in shallower water (2-5 m); recorded from exposed and moderately exposed sites at Lizard Island and other midshelf reefs.

Field identification. This species is easily distinguished when small by the unique combination of a single band and three stripes, and at larger sizes, by dark scale edges and distinct pale dots which lie in the region of the dark stripes.

Previous descriptions. The late juvenile phase has been described by Choat & Randall (1986). Burgess & Axelrod (1973b, p. 628, pl. 85) give a colour plate of a small scarid from the Maldives. This specimen is probably a juvenile *S. rubroviolaceus*.

Scarus schlegeli (Bleeker)

Pl. 2G,H

Material examined. (5 specimens: 16-38 mm). AUSTRALIA - Lizard Island, AMS I.25906-001 (1: 37 mm), AMS I.25782-001 (1:38 mm). Provisional identifications: AMS I.27849-010 (1:16 mm), AMS I.27816-003 (1:24 mm), AMS I.27818-001 (1:36 mm).

Diagnosis. Median predorsal scales 4, no anterior pair, anterior scale largest; cheek scale rows 2; pectoral rays 14.

Diagnostic colour notes. Small specimens uniformly black or dark grey-brown with pale snout; 4-5 thin pale vertical lines displayed most frequently by specimens greater than 50 mm.

Colour notes. At less than 20 mm, body and fins black to dark grey-brown; some small specimens (25-35 mm) provisionally identified as *S. schlegeli* displayed 3 indistinct stripes, but only briefly; typical colour at all sizes dark grey-brown, with pale grey snout; all specimens observed displayed 4-5 thin pale vertical lines which correspond with pale interspaces of 'typical' banded scarid pattern (Fig.4); intensity and duration of lines varies and may change rapidly, lines more distinct and more frequently displayed by individuals greater than 50 mm; large juveniles displaying thin pale vertical lines extremely similar to small IP specimens; IP colouration appears at approximately 110 mm, in IP vertical lines more distinct and body and fins often have browner hue; live colour patterns often fade shortly after collection (freshly collected specimen shown in Pl. 2G; Pl. 2H shows stressed pattern of captive specimen).

Colour in alcohol. Body and fins dark brown, occasionally indistinct body stripes, smaller specimens with dark dashes at base of dorsal and anal fins and occasionally at base of most dorsal and ventral caudal fin rays; as in live specimens, some patterns are indistinguishable from those of *S. psittacus*, precluding any identification further than *S. psittacus/schlegeli*.

Ecology. Uncommon, occasionally solitary, usually in small (approx. 5 individuals) to medium sized (greater than 15 individuals) conspecific or multispecies schools; settlement sites unknown; recorded only from relatively deep water (5-15 m), typically over low coral rubble on sand; most frequently observed at base of reef slope, in both exposed and sheltered locations, occasionally schooling with *S. sordidus* and *S. chameleon*.

Field identification. This species is often difficult to identify in the field, as it rarely displays the diagnostic pale vertical lines, especially individuals less than 40 mm. The two main species with which it may be confused are *S. sordidus* and *S. chameleon*, both of which often display uniformly dark colour patterns, especially in deep water and when in multispecies schools. *S. chameleon* may also have a pale snout, as in *S. schlegeli*. The three species can only be separated in the field when they display diagnostic colour patterns which may require extended observations. Provisional identifications may be checked using meristics, as these three species are readily separated by scale counts. Other dark coloured species including *S. gibbus*, *S. bleekeri* and *S. spinus* can be distinguished from *S. schlegeli* by their diagnostic colour patterns, and their more rounded profile. *S. spinus* and *S. schlegeli* also differ in their depth preferences, being restricted to shallow and deep areas respectively.

The main problem when identifying juvenile *S. schlegeli* is distinguishing them from juvenile *S. psittacus*. These two species have indistinguishable meristic values and although they differ greatly in their typical colour patterns and depth distributions there is some overlap in these parameters. The differences between the two species which will enable most specimens to be distinguished in the field are summarised below:

S. psittacus: often pale or striped, does not display vertical bands nor a uniformly black colouration. If the overall colour is brown (as in some larger specimens) the pelvic fins and, to a lesser extent, the anal fin have a red hue. Abundant in shallow water (1-5 m).

S. schlegeli: usually has a uniformly dark grey-brown or black body and fins; displays indistinct stripes extremely rarely. Occasionally displays narrow pale vertical lines (more often when greater than 50 mm). If the overall colour is brown, anal fin remains brown, and red hue in the pelvic fins is either indistinct or absent. Only abundant in deeper water (below 5 m).

The greatest difficulty was experienced in separating small uniformly brown specimens which have meristic counts corresponding to both *S. psittacus* and *S. schlegeli*. These specimens cannot, at present, be identified further and must remain as *S. psittacus/schlegeli*.

As in *S. psittacus*, positive identifications of *S. schlegeli* were restricted to individuals displaying diagnostic colour patterns in the field.

Previous descriptions. Choat & Randall (1986) describe the late juvenile phase and give a colour plate of a 110 mm specimen from Heron Island.

Scarus sordidus Forsskål

Pl. 2A,B

Material examined. (19 specimens: 9-66 mm). AUSTRALIA - Lizard Island, AMS I.27853-001 (1: 14 mm), AMS I.27854-001 (1:18 mm), AMS I.27816-001 (1:20 mm), AMS I.27816-002 (1:21 mm), AMS I.27854-002 (1:27 mm), AMS I.25798-002 (1:28 mm), AMS I.25793-002 (1:29 mm), AMS I.27823-001 to I.27823-004 (4:30-66 mm), AMS I.27825-001 (1:30 mm), AMS I.25786-001 (1:40 mm), AMS I.27819-004 (1: 43 mm), AMS I.27819-005 (1:51 mm), AMS I.25785-001 (1:56 mm), AMS I.27824-001 (1:60 mm). Provisional identifications: AMS I.27864-001 (1:9 mm), AMS I.27863-005 (1:10 mm).

Diagnosis. Median predorsal scales 4, no anterior pair, anterior scale largest; cheek scale rows 2; pectoral rays 14-16 (usually 15); dental plates exposed in larger specimens.

Diagnostic colour notes. Body uniformly dark-brown black or bearing 5 dark stripes; caudal fin base and caudal peduncle often pale with exception of dark caudal extremities of orbital and pectoral stripes which may be fused; larger specimens typically uniformly dark, caudal peduncle and caudal fin base often pale with a dark central dot.

Colour notes. Although colour patterns change greatly during ontogeny, basic colours are consistent; body or pale interspaces remain off white, dark stripes black, brown or green brown; sequence of colour patterns follows 'typical' scarid pattern outlined in Fig. 3, dashes in orbital and pectoral stripes start to fuse at about 12 mm, with complete fusion of all stripes by 21 mm, dorsal division of dorsal stripe fuses last; at 21 mm, caudal extremities of orbital and pectoral stripes may darken in some individuals but intensity varies markedly (Fig. 7A,B).

In progressively larger specimens, body and fins darken, and greater than 32 mm, may be uniformly black; caudal extremities of orbital and pectoral stripes expand and eventually fuse at about 40 mm, surrounding area is pale and gives characteristic appearance of pale patch on caudal peduncle and caudal base, with dark central dot (Fig. 7C,D; indistinctly visible in Pl. 2B).

Wide range of colour patterns may be displayed greater than 30 mm, from uniformly black to striped, with or without dark dot on caudal peduncle (Table 1); colour pattern may change rapidly, often in less than two seconds; greater than 50 mm, range of patterns may occasionally include 2 series of 3-4 white dots on posterior region of uniformly dark body; colour patterns of specimens greater than 60 mm essentially same as those of IP, with predominant colour pattern being uniformly dark brown-black; pale patch on caudal fin and caudal peduncle with dark central dot and series of pale dots on body often displayed by stressed individuals, especially if solitary, and often become increasingly distinct upon collection or shortly after death.

Colour in alcohol. Small specimens retain dashes or stripes, body off white to grey, stripes dark grey, dark caudal extremities of orbital and pectoral stripes retained and often prominent; larger specimens (greater than 40 mm), body and fins dark-grey brown, caudal fin base usually paler with dark central dot.

Ecology. Common; in small (comprising 5-15 individuals) conspecific or multispecies schools, occasionally solitary or in large (greater than 25 individuals) schools; site attached when small; settlement sites include live arborescent coral (primarily *Acropora*) and algal covered dead coral or coral rubble; recently settled specimens and small individuals in dashed or early striped phase (9-15 mm) often found in pomacentrid territories, particularly those with rich algal 'lawns', including *Plectroglyphidodon lacrymatus, Pomacentrus grammorhynchus, Stegastes nigricans* and *S. apicalis;* juveniles recorded over all substratum types, except open sand, in all reef habitats from 1-14 m; present on inner shelf reefs, abundant on mid- and outer shelf reefs; at Lizard Island, juveniles particularly abundant in lagoon, remaining within small home ranges until approximately 90 mm, before joining large mobile schools; despite large numbers of juveniles in lagoon, no IPs, TPs or juveniles greater than 92 mm recorded from this area during 25 month study period; Bellwood (1986) suggested that *S. sordidus* migrate from lagoon during late juvenile phase; detailed notes on biology of juvenile *S. sordidus* given in Bellwood (1986).

Field identification. An easily identified species when displaying the diagnostic pale caudal peduncle and caudal fin base with a dark central dot (Fig. 7C,D). However, two common colour patterns of *S. sordidus* are also displayed by other species (Table 1). When uniformly black, *S. sordidus* may be mistaken for *S. schlegeli* at sizes less than 30 mm, or *S. spinus, S. bleekeri* and *S. gibbus* at sizes greater than 30 mm. *Scarus schlegeli, S. spinus* and *S. gibbus* can be separated from *S. sordidus* using meristics but they can also be separated in the field. *Scarus sordidus* has a more rounded snout and deeper body than *S. schlegeli* and *S. spinus*, although this may be difficult to assess in solitary specimens. For a positive identification of a uniformly dark specimen, prolonged observations are usually necessary. *Scarus schlegeli, S. bleekeri* and *S. gibbus* all possess unique colour patterns, whilst *S. sordidus* (greater than 30 mm) frequently exhibits the unique pale caudal peduncle and caudal fin with a dark central dot, especially if disturbed. If a

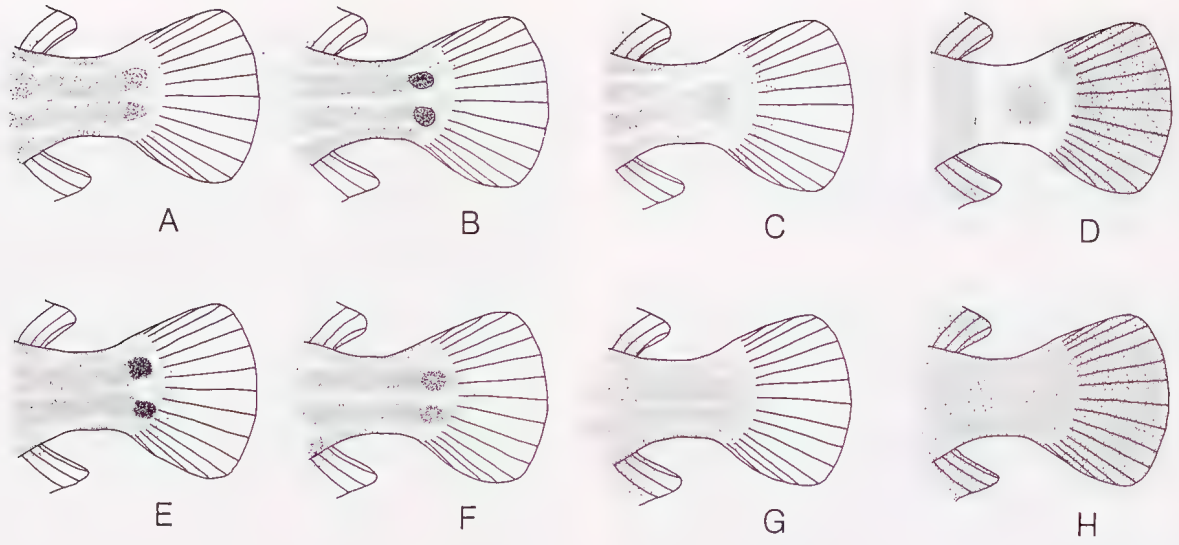


Fig.7. Ontogenetic changes in the colour pattern of the caudal region of *S. sordidus* and *S. spinus*. *S. sordidus:* A, 19 mm; B, 23 mm; C, 40 mm; D, 50 mm. *S. spinus:* E, 18 mm; F, 22 mm; G, 27 mm; H, 40 mm. See text for details of colour pattern changes.

uniformly black pattern is maintained by a large specimen (greater than 50 mm) for a prolonged period (hours or days) and the pectoral fins do not have a yellow hue (= *S. gibbus*), then the specimen is likely to be *S. spinus*, although meristic analyses are required before a positive identification can be made.

When striped, small *S. sordidus* (less than 30 mm) are difficult to distinguish from similarly sized *S. spinus*. There are, however, several slight differences that separate the two species. In *S. sordidus*, dashes in the dorsal division of the dorsal stripe fuse at a smaller size than in *S. spinus* (i.e. at about 20 mm, cf. 27 mm in *S. spinus*); the dark stripes are often paler, the pale interspaces darker, and the dark caudal extremities of the orbital and pectoral stripes less intense than in similarly sized *S. spinus*, especially less than 20 mm. In addition, *S. sordidus* typically has a deeper body and lacks the white patch at the caudal fin base, which is present in *S. spinus* (faintly visible in Fig. 7F; Pl. 2D). The diagnostic differences in the caudal region of these two species are summarised in Fig. 7. Despite these differences, it is often necessary to collect the specimen for meristic analysis to check field identifications. Other species which may display a striped pattern with dark caudal extremities of the orbital and pectoral stripes include *S. globiceps* and *S. chameleon*. These species may be initially confused with *S. sordidus*, however, this colour pattern is only rarely displayed by these species. Both species can be easily distinguished from *S. sordidus* (and *S. spinus*) by their pale body and the lack of a dorsal division of the dorsal stripe.

As with most other *Scarus* species which follow the 'typical' scarid sequence of colour pattern changes during the early post-settlement phase (Fig. 3), recently settled *S. sordidus* cannot be accurately identified in the field. Small individuals with dark dashes or stripes are likely to be *S. sordidus*, but these individuals must be grown to a larger size before an accurate identification can be made based on both the colour pattern and meristic values. Small specimens collected prior to the development of the head scales, may be tentatively identified as *S. sordidus* if they have (a) dark body dashes or stripes, (b) 15 pectoral fin rays, and (c) 3 upper pharyngeal tooth rows. It must be noted, however, that this combination is also possessed by *S. gibbus*, *S. bleekeri* and *S. pyrrhurus*.

Previous descriptions. Schultz (1958) described the ontogeny of the colour patterns of juvenile *S. sordidus*. However, these descriptions were based on preserved material and are therefore of limited use for field identifications. Choat & Randall (1986) describe the late juvenile phase, and provide a colour plate of a 37 mm specimen from Jana Island, Persian Gulf and a 50 mm specimen from Lizard Island.

Morphological notes. The identification of extremely small *S. sordidus* (less than 15 mm) may be supported by an examination of the upper pharyngeal tooth rows. *S. sordidus* possesses three rows on each upper pharyngeal bone, whereas all other GBR *Scarus* species, with the exception of *S. bleekeri*, *S. gibbus* and *S. pyrrhurus*, typically possess only two rows.

Scarus spinus (Kner)

Pl. 2C-E

Material examined. (25 specimens: 9-50 mm). AUSTRALIA - Lizard Island, AMS I.27827-001 (1: 15 mm), AMS I.27844-004 (1:17 mm), AMS I.25910-001 (1:20 mm), AMS I.25917-002 (1:20 mm), AMS I.27844-001 (1:21 mm), AMS I.25910-004 (1:22 mm), AMS I.27828-001 (1:23 mm), AMS I.25910-003 (2: 27 mm), AMS I.27839-007 (1:27 mm); Yonge Reef, AMS I.27829-007 to I.27829-010 (4:17-28 mm), AMS

I.25912-003 (1:21 mm), AMS I.25912-005 (1:27 mm), AMS I.27820-001 (1:50 mm). Provisional identifications: Lizard Island, AMS I.27848-001 (1:9 mm), AMS I.27846-001 (1:10 mm), AMS I.27846-002 (1:11 mm), AMS I.27847-003 (1:11 mm), AMS I.27836-002 (1:17 mm), AMS I.27847-002 (1:19 mm), AMS I.27821-001 (1:21 mm), AMS I.27821-002 (1:21 mm).

Diagnosis. Median predorsal scales 4, anterior scale relatively small, preceded by pair of laterally overlapping scales; cheek scale rows 3, 1-3 (usually 2) in ventral row; pectoral rays 14 (rarely 15); based on specimens greater than 20 mm.

Diagnostic colour notes. Body off white with 5 dark stripes; dorsal division of dorsal stripe remains dashed to 27 mm; posterior extremities of orbital and pelvic stripes form intense dark round dots in white patch at caudal fin base; greater than 35 mm, body and fins uniformly black.

Colour notes. A variable species, no rapid colour changes; small specimens invariably striped, body off white to pale grey with intense dark brown to black dashes or stripes; sequence of colour pattern changes during early postsettlement phase closely follows 'typical' scarid sequence outlined in Fig. 3; greater than 15 mm, intense dark stripes on pale body sole colour pattern to approximately 25 mm, although intensity of pale interspaces may vary; striped colour pattern characterised by 5 body stripes: 4 primary stripes, and dorsal division of dorsal stripe, stripes relatively narrow and dark, with more contrasting appearance than other striped *Scarus* species; stripes much darker in field than in Pl. 2C,D; posterior extremities of orbital and pectoral stripes intense black (Fig. 7E), with contrast enhanced at approximately 20-25 mm as caudal extremities lie in white hemispherical patch on caudal fin base (Fig. 7F), patch more intense in field than in Pl. 2D, closely resembling patch in *S. niger* (Pl. 5F); intense caudal extremities of medial body stripes first displayed at approximately 15 mm, remaining until about 25 mm when start to diffuse (Pl. 2E), these changes summarised in Fig. 7E—G; greater than 25 mm, contrast between dark stripes and pale interspaces decreases and fins darken (Pl. 2E; Fig. 7H), uniformly black body may be displayed by specimens greater than 30 mm, almost invariably displayed by specimens greater than 40 mm; this pattern continues through to IP, pale vertical lines displayed by some IP specimens (Choat & Randall, 1986) not present in juveniles or small IP specimens observed on Lizard Island.

Colour in alcohol. Live colour pattern retained, although colours fade; pale interspaces grey, stripes dark grey; less than 25 mm, dashed dorsal division of dorsal stripe and dark posterior extremities of orbital and pectoral stripes remain distinct; greater than 30 mm, colour pattern indistinct, body and fins uniformly dark grey-brown.

Ecology. Uncommon; solitary or in small multispecies schools; site attached; small and recently settled specimens most often recorded in live arborescent corals, few specimens recorded within pomacentrid territories; on Lizard Island, small juveniles recorded in shallow water (2-5 m), in areas with abundant live coral, typically in sheltered areas, occasionally in semi-exposed locations; most juveniles recorded from lagoon, but only individuals less than 50 mm, larger juveniles and adults absent from this area, absence may indicate migration as in *S. sordidus;* on outer reefs, occasionally observed over live coral or coral rubble, on slopes and bases of backreef bommies (3-9 m).

Field identifications. *Scarus spinus* closely resembles *S. sordidus,* and in the field the two species may be confused. There are, however, several slight differences in the colour patterns of the two species which enable some individuals to be identified in the field but, because of the degree of overlap, collection and diagnostic meristic analyses are recommended. When the two species are compared in the field, *S. spinus* has a more elongate body, darker, narrower stripes, and a more distinctly dashed dorsal division of the dorsal stripe (especially when viewed from above). In comparison, *S. sordidus* has a deeper body, broader, less contrasting dark body stripes, and an indistinctly dashed dorsal division of the dorsal stripe. In addition, the intense dark caudal extremities of the medial body stripes have a characteristic form in both species. In *S. spinus,* the dark extremities are intense and contrast strongly with the adjacent white patch(es), especially at 15-25 mm. In *S. sordidus,* the extremities are less intense and the contrast with surrounding pale patches less notable than in *S. spinus;* the stripes anterior to the dark extremities are often faded and the dark extremities more diffuse. These differences are summarised in Fig. 7. The differences are clearest in specimens between 15-30 mm; less than 15 mm, identifications must be verified by meristic characters (primarily pectoral ray counts). At sizes greater than 30 mm, *S. sordidus* can be distinguished by the characteristic dark dot on the caudal peduncle. A specimen with a uniformly black pattern may be one of several species, including *S. bleekeri, S. gibbus, S. schlegeli, S.sordidus* and *S. spinus* (Table 1). Larger juvenile *S. spinus* have a more rounded snout than these species, which may aid identification, but there are no diagnostic colour patterns displayed by *S. spinus* greater than 30 mm. A uniformly black specimen in shallow water (1-5 m) which retains this pattern for extended periods, even if chased, is likely to be *S. spinus* although meristic verification is essential.

Previous descriptions. The late juvenile stage of *S. spinus* was described briefly by Schultz (1958; as *S. formosus* Valenciennes), but based only on preserved material.

Discussion

Juvenile scarids on the Great Barrier Reef exhibit a wide range of colour patterns. Within this range, there are two distinct groups characterised by a strong correlation between juvenile colour patterns, range of patterns exhibited at a given size, extent of change throughout

ontogeny, speed of colour pattern changes, and social behaviour and habitat as a juvenile.

The two groups represent the extremes of a spectrum of juvenile scarid types. The first group is solitary and are characterised by: (a) complex colour patterns which are often cryptic and/or camouflaged in the field, (b) an inability to change colour patterns rapidly, and (c) the presence of several different patterns throughout ontogeny, although only one at a given size. These species are typically site attached, and live in areas of high topographic complexity. As adults, species in this group are typically either solitary or haremic. This group is exemplified by *S. frenatus, S. niger* and *S. altipinnis,* and to a lesser extent *C. carolinus, S. dimidiatus* and *S. oviceps.*

The second group are typically schooling and are characterised by: (a) simple colour patterns which are either striped, barred or uniformly plain, (b) an ability to change colour patterns rapidly, with several colour patterns being displayed at a given size, and (c) only a limited number of colour pattern changes during ontogeny. These species are site attached when small, become highly mobile in the late juvenile phase, and typically live in areas of relatively low topographic complexity. These species constitute the abundant schools of small grey scarids that occur in large numbers in shallow reef areas. As adults, species in this group usually remain highly mobile, forming moderately large multispecies schools. This group is exemplified by *S. psittacus, S. rivulatus* and *S. globiceps,* and to a lesser extent *S. ghobban, S. sordidus, S. schlegeli* and *S. chameleon.*

The two groups clearly demonstrate the problems encountered when identifying juvenile scarids. Species in the first group may not initially look like scarids and their solitary behaviour and cryptic nature make them easy to overlook. Once located, however, they are readily identified. Species in the second group are ubiquitous and represent what are, for most workers, the typical small uniformly grey-brown or striped juvenile *Scarus* species. These species are easily located, but subsequent identification requires extended observation and an eye for the subtle minutiae that enable one to distinguish species in the field. In many cases field identifications must remain tentative. If collected, most species can be identified, with the notable exceptions of the *S. schlegeli/ psittacus* and *S. rivulatus/ globiceps* pairs.

In addition to the groups described above, there is a range of species in-between which have either intermediate character states or possess features associated with both groups. Such intermediate species include *S. rubroviolaceus, S. flavipectoralis, S. gibbus, S. bleekeri* and *S. forsteni.* The above grouping excludes *C. bicolor* and *H. longiceps.* These species have unusual colour patterns which show similarities to the juvenile stages of other reef species. The possibility of these colour patterns having a mimetic function requires further investigation.

The status of some species in relation to these groups appears to vary with size and geographic location, but observations and descriptions of juvenile scarids from other geographic regions suggests that the above groups are typical for the family as a whole.

There are a number of explanations that may account for the observed range of juvenile colour patterns, including phylogenetic constraints and their function as predation avoidance mechanisms. Some closely related species have extremely similar colour patterns, e.g. *S. dimidiatus* and *S. oviceps,* but so have some distantly related species, e.g. *S.sordidus* and *S. spinus.* Although phylogenetic or developmental factors may determine the possible range of colour patterns, i.e. the typical scarid arrangement of dots and stripes, the influence of these factors appears to be limited. One of the more important factors appears to be the function of the colour patterns in predation avoidance. Scarids are prey for a wide range of diurnally active visual piscivores, including scorpaenids (Hiatt & Strassburg, 1960), serranids (Choat, 1968), carangids (Popova & S'erra, 1983) and sharks (Stevens, 1984), and during the juvenile phase probably have particularly high mortality rates (Bellwood, 1986). Most colour patterns are camouflaged and/or cryptic and make the individuals hard to locate in the field. Complex colour patterns may blend with the heterogeneous reef background whilst striped, barred or plain colour patterns may facilitate protection from predators in open areas, especially when schooling. The potential advantages, in terms of predation avoidance, of a striped colour pattern and a high degree of similarity between multispecific schooling species has been noted by Barlow (1972) and Ehrlich & Ehrlich (1973).

In some species at least, it also appears that colour patterns may have a social function, influencing the response of other species within the same trophic level. The interactions between juvenile scarids possessing various colour patterns and territorial pomacentrids is an area of particular interest.

Conclusions about the functions of colour patterns await a comprehensive study of the function and development of colour patterns in the family.

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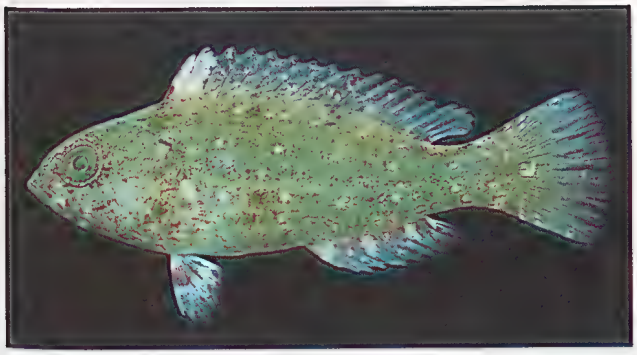
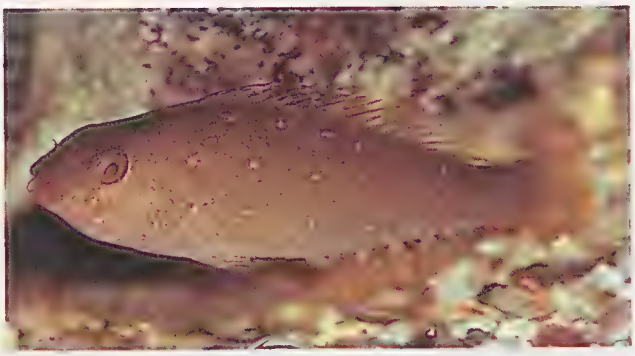


1A. *Calotomus carolinus*, 43 mm SL, AMS I.25905-002, dead, Lizard Island.



1B. *Leptoscarus vaigiensis*, approx. 50 mm SL, underwater photograph by R. Kuiter, Sydney Harbour.

1C. *Cetoscarus bicolor*, approx. 40 mm SL, underwater photograph by D.R. Robertson, Heron Island.

1D. *Hipposcarus longiceps*, 48 mm SL, AMS I.25783-001, dead, Lizard Island.

1E. *Scarus gibbus*, 25 mm SL, AMS I.25913-001, live, Lizard Island.

1F. *S. gibbus*, 40 mm SL, AMS I.25905-001, dead, Lizard Island.

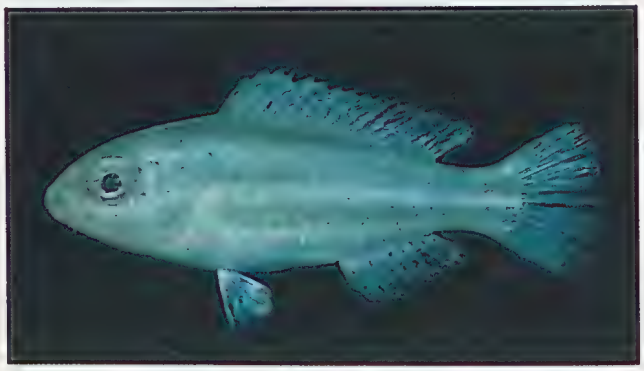
1G. *S. bleekeri*, 33 mm SL, AMS I.25916-001, dead, Lizard Island.

1H. *S. bleekeri*, 46 mm SL, AMS I.25903-002, dead, Lizard Island.

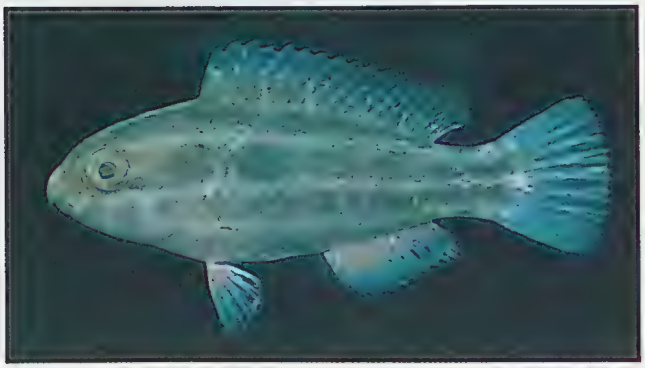
2A. *Scarus sordidus*, 28 mm SL, AMS I.25798-002, dead, Lizard Island.

2B. *S. sordidus*, 40 mm SL, AMS I.25786-001, dead, Lizard Island.

2C. *S. spinus*, 20 mm SL, AMS I.25910-001, dead, Lizard Island.



2D. *S. spinus*, 22 mm SL, AMS I.25910-004, dead, Lizard Island.



2E. *S. spinus*, 27 mm SL, AMS I.25912-005, dead, Yonge Reef.

2F. *S. psittacus*, 30 mm SL, dead, Lizard Island.

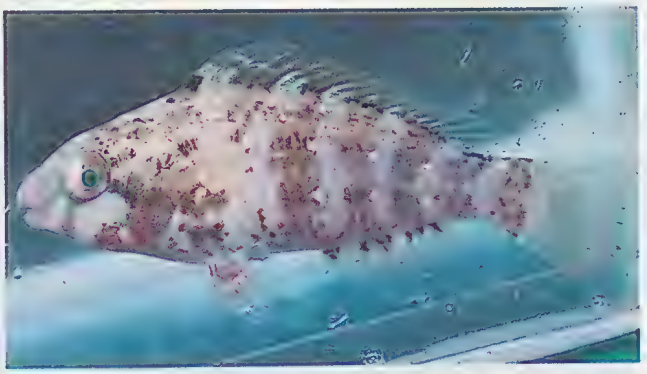
2G. *S. schlegeli*, 37 mm SL, AMS I.25782-001, dead, Lizard Island.

2H. *S. schlegeli*, 37 mm SL, AMS I.25906-001, live, Lizard Island.

3A. *Scarus flavipectoralis,* 33 mm SL, AMS I.25782-004, dead, Lizard Island.

3B. *S. flavipectoralis,* 44 mm SL, AMS I.25787-001, dead, Lizard Island.

3C. *S. chameleon,* 33 mm SL, AMS I.25793-001, dead, Lizard Island.



3D. *S. longipinnis,* 39 mm SL, AMS I.25789-001, live, Lizard Island.

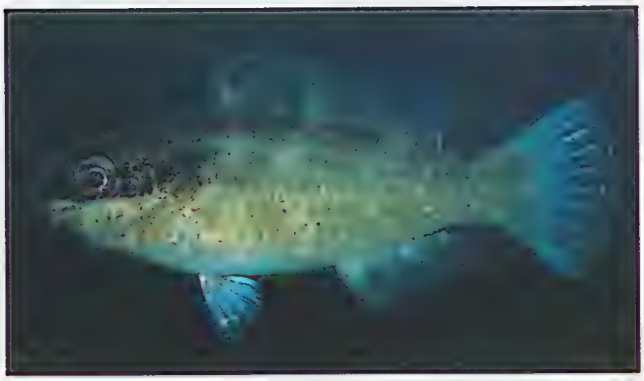
3E. *S. longipinnis,* 75 mm SL, AMS I.25784-001, dead, Carter Reef.

3F. *S. rubroviolaceus,* 18 mm SL, AMS I.25790-001, dead, Lizard Island.

3G. *S. rubroviolaceus,* 22 mm SL, AMS I.25909-003, dead, Lizard Island.

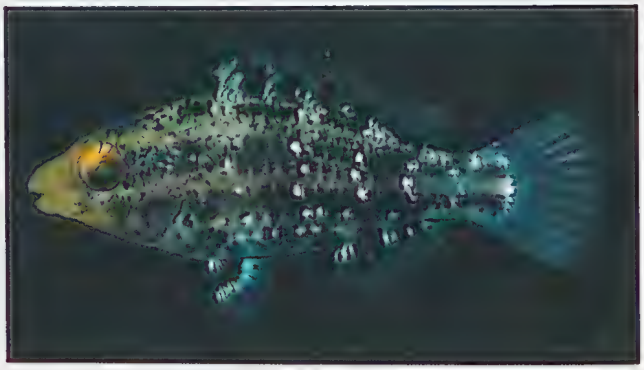
3H. *S. rubroviolaceus,* 38 mm SL, AMS I.25902-001, dead, Lizard Island.

4A. *Scarus dimidiatus*, 30 mm SL, AMS I.25912-006, dead, Yonge Reef.



4B. *S. oviceps*, 32 mm SL, AMS I.25794-002, dead, Lizard Island.

4C. *S. oviceps*, 73 mm SL, AMS I.25794-001, dead, Lizard Island.



4D. *S. altipinnis*, 26 mm SL, AMS I.25912-007, live, Yonge Reef.

4E. *S. altipinnis*, 29 mm SL, AMS I.25909-001, dead, Lizard Island.

4F. *S. altipinnis*, 54 mm SL, AMS I.25903-001, dead, Lizard Island.

4G. *S. altipinnis*, approximately 80 mm SL, underwater photograph by D.R. Robertson, Heron Island.

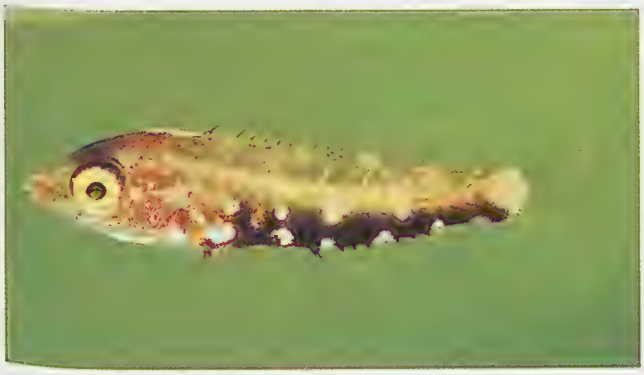
4H. *S. ghobban*, 52 mm SL, AMS I.25903-003, dead, Lizard Island.

5A. *Scarus rivulatus*, 49 mm SL, AMS I.25788-001, dead, Lizard Island.

5B. *S. frenatus*, 10 mm SL, AMS I.25914-001, live, Lizard Island.

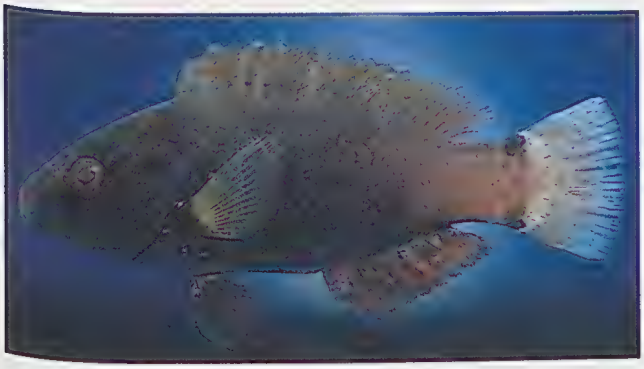
5C. *S. frenatus*, 23 mm SL, AMS I.25912-002, live, Yonge Reef.

5D. *S. frenatus*, 31 mm SL, AMS I.25912-001, live, Yonge Reef.



5E. *S. niger*, 10 mm SL, live, Lizard Island.

5F. *S. niger*, 34 mm SL, live, Lizard Island.



5G. *S. niger*, 57 mm SL, AMS I.25907-001, dead, Yonge Reef.

5H. *S. forsteni*, 61 mm SL, AMS I.25908-001, dead, Yonge Reef.

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Australian Aplacophoran Molluscs: I. Chaetodermomorpha from Bass Strait and the Continental Slope off South-eastern Australia

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ABSTRACT. Four new species of Chaetodermatidae (*Chaetoderma usitatum, Falcidens chiastos, F. lipuros* and *F. macrafrondis*) and a new genus and species of Prochaetodermatidae (*Rhabdoderma australe*) are the first Chaetodermomorpha described from off Australia; all are from the shelf in Bass Strait or from the continental slope off southeastern Australia. Two species are numerous: *F. chiastos* occurs at densities sometimes up to 180 m^2 from 22 to 120 m in 20 of the 23 shelf samples that contain Chaetodermomorpha, and the prochaetodermatid *R. australe* is common from deeper water, 1,120 to 2,510 m. Several additional species only recently received or with a single specimen are noted but not described; three belong to *Prochaetoderma, Limifossor,* or *Scutopus,* thereby extending the recorded ranges of these genera to the western Pacific. Of the 16 species of Chaetodermomorpha collected, four are shelf species occurring at depths of less than 200 m (*F. chiastos, F. lipuros,* one Prochaetodermatidae, one undetermined), six are upper slope species extending to 1,000 m (three species of *Falcidens, Chaetoderma* sp., *Scutopus* sp., *Limifossor* sp.) and six extend below 1,000 m (*C. usitatum, F. macrafrondis, R. australe, Falcidens* sp., *Chaetoderma* sp., *Prochaetoderma* sp.). These depth distributions are similar to other Pacific Chaetodermomorpha genera except for *Chaetoderma,* a genus usually common on the shelf but missing from Bass Strait.

SCHELTEMA, A.H., 1989. Australian Aplacophoran Molluscs: I. Chaetodermomorpha from Bass Strait and the Continental Slope off south-eastern Australia. Records of the Australian Museum 41(1): 43-62.

Aplacophoran molluscs belonging to the footless, burrowing group comprising the subclass Chaetodermomorpha (= Caudofoveata) have not been reported before from off Australia. Five species in two families and three genera are described here from recent collections made on the slope off southeastern Australia and the shelf in Bass Strait.

Materials

A total of 231 specimens in 27 samples were examined: 23 samples were taken between 22 and 130 m in Bass Strait, three samples from the continental slope off south-east Victoria between 1,120 and 2,510 m, and one sample from 1,200 m off Wollongong, New South Wales (Table 1). Twenty five of the Bass Strait stations are part of the Museum of Victoria Bass Strait Survey (RV *Hai-Kung,* FV *Sarda,* RV *Tangaroa*); one sample from the Bass Strait (Esso-Gipps Stn 20) and one sample from off Wollongong (FRV *Kapala*) comprise part of the collection of the Australian Museum (AM C149631 and AM C149638, respectively). In addition, 937 specimens from 17 stations taken by the Museum of Victoria between 363 and 1,850 m on the slope off Point Hicks (RV *Franklin*) have been

recently received and cursorily examined; a few data from these stations are included here (slope stations 25 and 27, Table 1; Discussion).

Methods

Descriptions of Chaetodermomorpha are based on external morphology, including measurements of body divisions, shape of oral shield, and attitude of spicules on the body wall; morphology of spicules; and morphology of entire, isolated radulae (see Scheltema, 1976, 1985, for more complete accounts of descriptive and statistical methods). Measurements of specimens were made with dividers on lines drawn lengthwise and crosswise on microscope images using a camera lucida attached to a dissecting microscope. The oral shield index is calculated by [(length x width) ≠ greatest trunk diameter x 100].

Spicules were removed by teasing after placing the specimen in a drop of glycerine in a depression slide; drawings were made using a camera lucida. Thickness was determined by using cross-polarised light, and lines were drawn between selected colour bands, or isochromes (Scheltema, 1985). Figure 1A shows morphological characters of a spicule.

Radulae were isolated by dissecting out the buccal mass and removing the tissue with sodium hypochlorite in a depression slide; after thorough rinsing, a drop of glycerine was added. Small radulae were removed in a drop of glycerine to a flat slide and examined under a coverslip.

Permanent slides were made of spicules from the holotype and of spicules and radulae from paratypes. Spicules were teased directly onto a slide and air-dried before mounting in a standard histologic mountant. Radulae were retrieved from the glycerine preparation, washed in distilled water in a depression slide, and run through a dehydration series before mounting.

Scanning electron microscope photographs were taken of holotype spicules using a JEOL JSM-840 microscope (Fig. 2).

Types and paratypes are deposited in either the Museum of Victoria, Melbourne (MV) or the Australian Museum,

Table 1. Specimens examined. C.u. = *Chaetoderma usitatum*; F.C. = *Falcidens chiastos*; F.l. = *Falcidens lipuros*; F.m. = *Falcidens macrafrondis*; R.a. = *Rhabdoderma australe*; P. sp = *Prochaetoderma* sp.; Sp.undet. = Species undertermined.

Cruise [1] and Stn	Gear [2]	Date	Depth m	Lat. S	Long. E	Sediment [3]	C.u.	F.c.	F.l.	F.m.	R.a.	P. sp	Sp. undet.
Sa80-113	S-M	3/11/80	66	40°23.9'	145°32'	msh		1					
HK-139	T	7/2/81	55	40°43.8'	148°32.7'	s							1
T-155	ES	12/11/81	70	38°56.0'	145°16.6'	m		12					
T-155	S-M	12/11/81	70	38°55.5'	145°17.0'	m		9					
T-156	ES	13/11/81	74	39°45.9'	145°33.5'	m		13					
T-156	S-M	13/11/81	74	39°45.9'	145°33.3'	m		18					
T-157	ES	13/11/81	75	40°10.9'	145°44.3'	m		7					
T-157	S-M	13/11/81	75	40°10.9'	145°44.3'	m		1					
T-158	ES	13/11/81	82	39°48.6'	146°18.8'	m		38					
*T-159	ES	13/11/81	80	*39°46.0'	*146°18.0'	m		*64					
T-159	S-M	13/11/81	80	39°43.5	146°18.8'	m		7					
T-163	ES	14/11/81	56	43°43.9	148°32.5	ms		1					
T-163	S-M	14/11/81	56	43°43.9'	148°32.5'	ms							1
T-165	ES	14/11/81	60	40°13.8'	148°39.6'	ms		1					
T-165	S-M	14/11/81	60	40°14.4'	148°30.0'	ms		1					
T-166	S-M	14/11/81	22	40°06.8'	148°24.4'	sh		1					
T-169	ES	15/11/81	120	39°02.4'	148°30.6'	sm		4	1				
*T-170	S-M	15/11/81	130	*38°57.8'	*148°26.5'	ms			*2				
T-179	ES	18/11/81	55	39°03.2'	146°39.5'	ms		1					
T-180	ES	18/11/81	65	39°12.9'	146°27.3'	ms		1					
T-181	ES	19/11/81	79	38°39.8'	144°18.2'	fs		3					
T-181	S-M	19/11/81	79	38°39.8'	144°18.2'	fs		10					
T-Q631	P	15/11/81	1120	38°35.1'	148°36.8'	sm					1	1	1
T-Q634	P	16/11/81	2510	38°42.3'	148°48.0'	m					1		
T-Q635	P	16/11/81	1730	38°55.6'	148°46.4'	scl					6		
E-G 20	n.d.	5/69	95	39°00.0'	148°24.8'	s		6					
*K76-23-02	n.d.	13/12/76	1200	*34°27-26'	*151°27'	n.d.	*6			*2	*9		
F-Slope 25	ES	22/7/86	1850	38°25.9'	148°58.6'	m	1				5		
F-Slope 27	ES	22/7/86	1500	38°26.0'	149°00.0'	cl	6				47	4	
Totals							13	199	3	2	69	5	3

[1] Sa80 = F.V. *Sarda*, Nov. 1980; HK = RV *Hai-Kung*, Feb. 1981; T = RV *Tangaroa*, Nov. 1981; E-G = *Esso-Gipps*, May 1969; K76 = FRV *Kapala*, Dec. 1976; F = RV *Franklin*, July 1986.

[2] S-M = Smith-MacIntyre grab, 0.1 m²; ES = epibenthic sled; P = pipe dredge; T = trawl.

[3] cl = clay; fs = fine sand; m = mud; ms = muddy sand; msh = muddy shell sand; s = sand; scl = silty clay; sh = shell; sm = sandy mud.

* Type locality

Sydney (AM).

Systematics

Chaetodermomorpha Pelseneer, 1905

Chaetodermomorpha Pelseneer, 1905
Caudofoveata Boettger, 1956

Diagnosis. Aplacophora lacking ventral furrow and foot; with oral shield as extension of pharyngeal cuticle (Scheltema, 1981, 1988) and with paired gills in cloaca (mantle cavity); often with distinct narrow constriction anteriorly; stomach and digestive gland differentiated from each other (Scheltema, 1981); radula distichous with bipartite or fused (unipartite) radular membrane (Scheltema, 1981, 1988), or radula specialised into a cone with a pair of denticles (Scheltema, 1972); spicules solid and more or less leaf-shaped; with distinct or indistinct dorsoterminal sensory organ (Haszprunar, 1987).

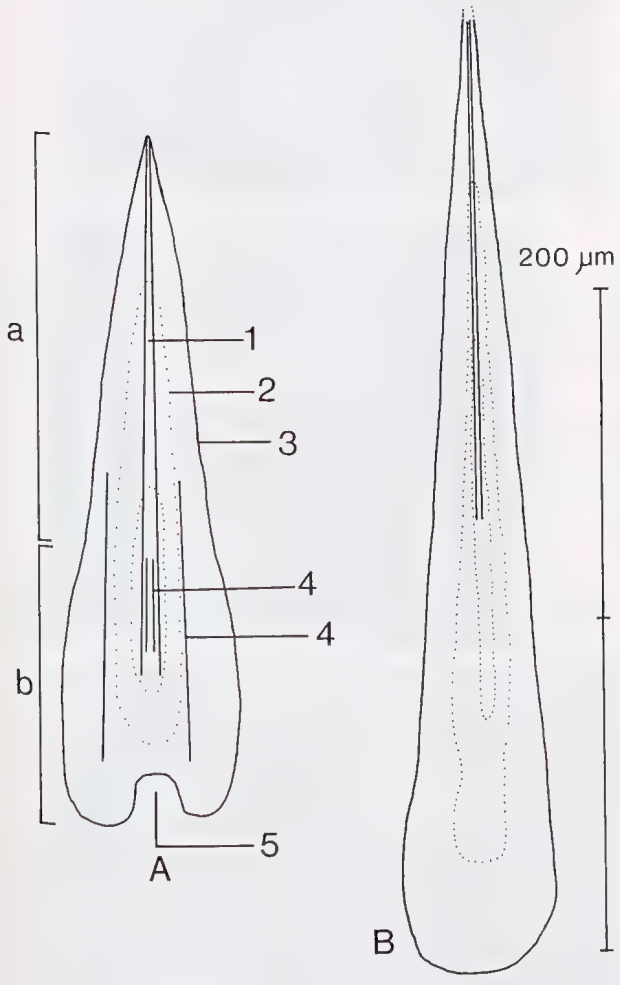

Fig.1. A: Generalised spicule, distal end at top, showing morphology: 1, medial keel; 2, isochrome (line between two color bands) as seen under cross-polarised light; 3, side edge; 4, ridges; 5, basal notch; a, blade; b, base; the waist lies between a and b. Spicule length is the distance between most proximal and most distal points; width of blade and of base is the greatest distance between their side edges. B: Spicule of *Prochaetoderma* sp. from Stn Q631 (see Table 1); greatest thickness 9 µm.

Chaetodermatidae Marion, 1885

Diagnosis. Chaetodermomorpha having a cone-shaped radula with a pair of denticles; arrangement of internal organs and musculature reflected externally by 4 body divisions: neck, anterior trunk, posterior trunk, and posterium, which vary among species in length relative to total body length; anterior constriction between neck and anterior trunk usually obvious (Figs 3, 10).

Chaetoderma Lovén, 1844

Chaetoderma Lovén, 1844.
Crystallophrisson Möbius, 1875.-Ivanov, 1981. (See Heppell, 1963; Bulletin of Zoological Nomenclature, 1966, Opn 764; Salvini-Plawen, 1984.)

Type species. *Chaetoderma nitidulum* Lovén, 1844, by monotypy.

Diagnosis. With characters of the family. Radula with paired denticles lying outside dome-shaped membrane which covers the buccal mass and with paired lateral projections extending from radula cone to dome-shaped membrane opposite base of denticles (Fig. 5).

Distribution. World ocean except Antarctic, especially near coasts.

Chaetoderma usitatum n.sp.

Figs 2A, 2B, 3, 4, 5; Table 1

Type material. HOLOTYPE: off Wollongong, NSW, 34°27-26'S, 151°27'E, 1,200 m. AM C156232 (wet specimen, spicule slide. Second spicule slide MV F54194). PARATYPES 1, 2: type locality. AM C156233 (1), C156234 (2).

Diagnosis. Large, up to nearly 3 cm in length, posterior trunk half or less total length, up to about 2 mm in diameter, longer and wider than anterior trunk; spicules up to 400 µm long, greater than 100 µm thick in all body regions, thickest medially with broad keel, flared base, distinct waist, and narrow blade, those of neck and anterior trunk bent outwards and held perpendicular to body wall with sediment densely packed between them, those of posterior trunk flat lying; radula large, up to 550 µm in total length and two fifths neck diameter, lateral projections short, 40-60 µm, dome-shaped membrane extending one third distance along

cone, cone nearly square in cross-section, 150 by 190 µm, denticles about 50 µm.

Etymology. From *usitatum,* meaning usual.

Description. *External morphology. Chaetoderma usitatum* is largest Chaetodermomorpha in samples from off south-east Australia ranging up to nearly 3 cm in length (Fig. 3); smallest specimen in collection measures 7.1 mm. Body conforms to a shape common for genus *Chaetoderma.* Neck is short, one tenth body length; anterior trunk shorter than posterior trunk, which is one half or less body length; posterium less than one tenth body length. Anterior trunk widest at usually distinct anterior constriction. Neck and anterior trunk about same diameter, up to 1.5 mm; diameter of posterior trunk nearly one and one half times that of greatest anterior trunk diameter and measures up to 1.9 mm.

Spicules of neck and anterior trunk held perpendicular to body wall and are scarcely visible because of sediment

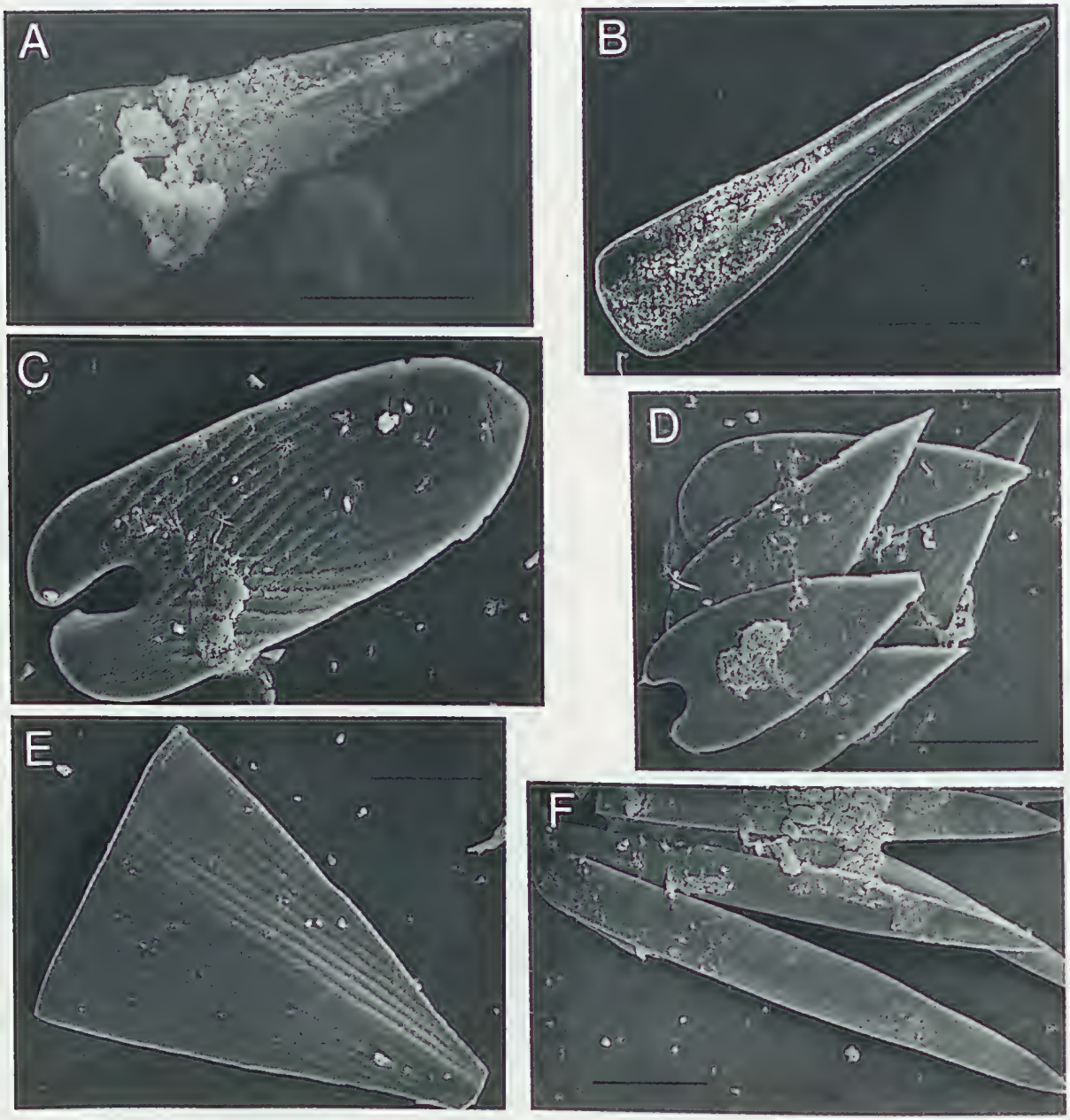

Fig.2. Spicules from holotypes of: A: *Chaetoderma usitatum* n.sp., body region 'e' (see Fig.4); B: *C. usitatum,* region 'g'; C: *Falcidens chiastos* n. sp., region 'e' (see Fig. 7); D: *Falcidens lipuros* n.sp., between regions 'd' and 'e' (see Fig. 11); E: *Falcidens macrafrondis* n.sp., distal half of large trunk spicule (see Figs 13A, 14); F: *Rhabdoderma australe* n.sp., body region c^1 (see Fig. 16), showing fine longitudinal striations. Scale bars = 50 µm.

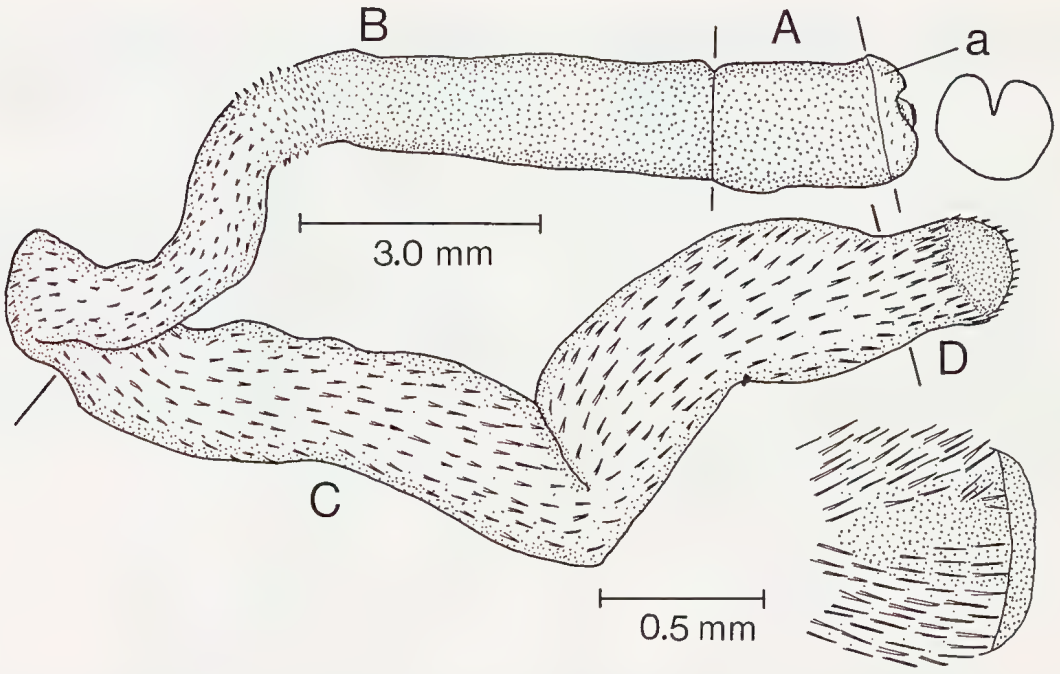

Fig.3. *Chaetoderma usitatum* n.sp., holotype, with oral shield and posterium/cloaca shown enlarged. Coarse stippling indicates sediment packed between the spicules; sediment perhaps covers the dorsoterminal sensory organ of the posterium, which is drawn in dorsal view. Body divisions are a, anterium; A, neck; B, anterior trunk; C, posterior trunk; D, posterium.

packed between them from distal tips to cuticle. Spicules of posterior trunk flat lying and easily dislodged, leaving body translucent where they are missing.

Anterium and oral shield usually exposed; oral shield of moderate size for genus and has short dorsal cleft.

Cloaca flattened on posterior end and packed with sediment; spicules of cloaca not noticeably longer than those of posterium and do not form discrete ring. Dorsoterminal sensory organ not evident, probably hidden by sediment.

Holotype: total length 26.3 mm; anterium 0.3 mm long; neck 2.1 mm long by 1.4 mm in diameter; anterior trunk, which is stretched beyond natural condition, is 11.5 mm long by 1.3 mm in diameter; posterior trunk 11.2 by 1.9 mm; posterium 1.2 by 0.7 mm; oral shield is 0.35 mm in width by 0.30 mm in height; index 5.53.

Spicules. Spicules from all body regions thickest medially, greater than 10 µm, with usually broad, flared base, distinct waist, relatively narrow blade with distinct, broad keel (Figs 2A and B, 4). Lengths increase from about 100 µm on neck (region 'b') to about 400 µm on posterior part of posterior trunk (region 'h'). Spicules from neck and anterior part of anterior trunk (regions 'b'-'d') are bent outward at a 20-30° angle; those from posterior part of anterior trunk are less bent (region 'e'); and those from posterior trunk (regions 'f'-'h') are nearly flat, slightly bent toward body. Thickest part of spicule shifts from base in spicules from anterium, neck and most anterior trunk (regions 'a', 'b', 'c') to waist in spicules from trunk regions 'e'-'h' and back to proximal end on spicules from posterium (region 'i'). Base and blade are of about equal length on bent spicules from neck and anterior trunk ('b'-'e'); blade becomes relatively longer on nearly flat spicules of posterior trunk ('f'-'h'). Base widths of bent trunk spicules ('c', 'd') more than 2 to 3 times blade width and bases flared, i.e., widest part proximal. In spicules of neck ('b'), midtrunk ('e') and posterior trunk ('f'-'h'), base width 2 times blade width or less. Two types of spicules predominate in mid- and posterior trunk regions ('e'-'h'): in one, edges of base flared; in other, edges of base nearly parallel. Blades of latter type narrower than those of former. Third type of spicule found scattered throughout trunk: short, with edges of base and blade very convex and blade wide relative to base.

Besides keel, ornamentation restricted to ridge parallel to each edge from below waist to midblade; a few short ridges are present on keel of some spicules from mid- and posterior trunk ('e'-'h').

Spicules of posterium ('i') long (more than 300 µm), narrow (less than 50 µm), without waist, bluntly pointed; some short, thin, sharply keeled, asymmetric spicules with one edge more curved than other, tapered proximally, also present.

Radula. Two radulae were examined (Fig. 5). Radula large, 500 and 550 µm in total length, nearly two fifths neck diameter. Cone of one radula is 470 µm long and nearly square in cross-section, 150 µm wide on anterior and posterior sides and 190 µm laterally (see description of radula under *Falcidens chiastos* below for orientation). Lateral projections very short, 40 to about 60 µm. Dome-shaped membrane (200 and 275 µm) extends about one third of distance along cone. Denticles, seen clearly in only one radula, are 52 µm.

Distribution. The species is known from 13 specimens taken between 1,200 and 1,850 m off Point Hicks, Victoria, and off Wollongong, New South Wales (Table 1).

Closely related species. *Chaetoderma californicum* Heath, 1911 is a north-eastern Pacific species taken from between 1100 and 1200 m off San Diego, California (holotype, known only from slides) and from 800 m (1 specimen) and 1600 m (2 specimens) off the coast of Oregon. (The holotype slides and Oregon specimens have been examined but a redescription of the species has not yet been published.). *Chaetoderma californicum* is similar to *C. usitatum* in general body shape and size, in morphology of the posterior trunk spicules, and in size of the radula. However, the anterior trunk spicules of *C. usitatum* have a longer and narrower blade than those of *C. californicum*, the neck is shorter relative to total body length, and the oral shield is smaller. In *C. californicum* the ratio of posterior to anterior trunk width (2 times) is greater than in *C. usitatum* (1.5 times) and the length of the lateral projection of the radula is up to 2 times greater.

Chaetoderma sibogae (Stork, 1941) [=*C. indicum* (Stork)] from 959 and 1,886 m in the Java Sea is similar in body shape, and the posterior part of the anterior trunk is similarly distorted by stretching, but the species is too poorly described for a more precise comparison. *Chaetoderma akkesiensis* Okuda, 1943 from 54 m off Japan is likewise similar in shape, but the illustrated spicules are dissimilar, as are those of *Chaetoderma militare* Selenka, 1885 from the Philippines (genus of the latter is uncertain, and the species is poorly described).

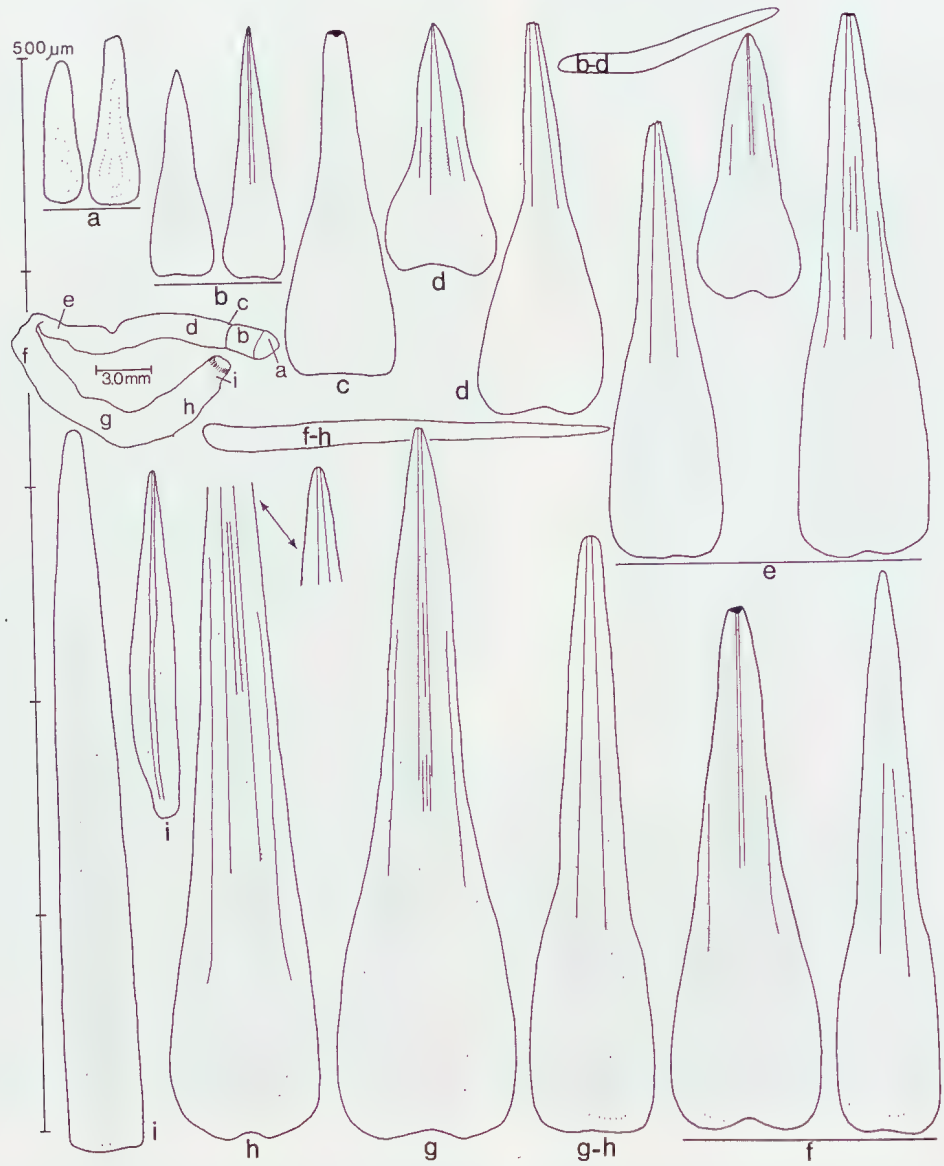

Fig.4. Spicules of *Chaetoderma usitatum* n.sp., paratype no. 1 (illustrated at middle left), from the anterium ('a'), neck ('b'), anterior trunk ('c'-'e'), posterior trunk ('f'-'h'), and posterium ('i'). Side views are labelled 'b'-'d' and 'f'-'h'; distal end is to the right, outer surface is above. Greatest thickness is greater than 10 µm for all body regions, but most from the anterium ('a') are 10 µm or less.

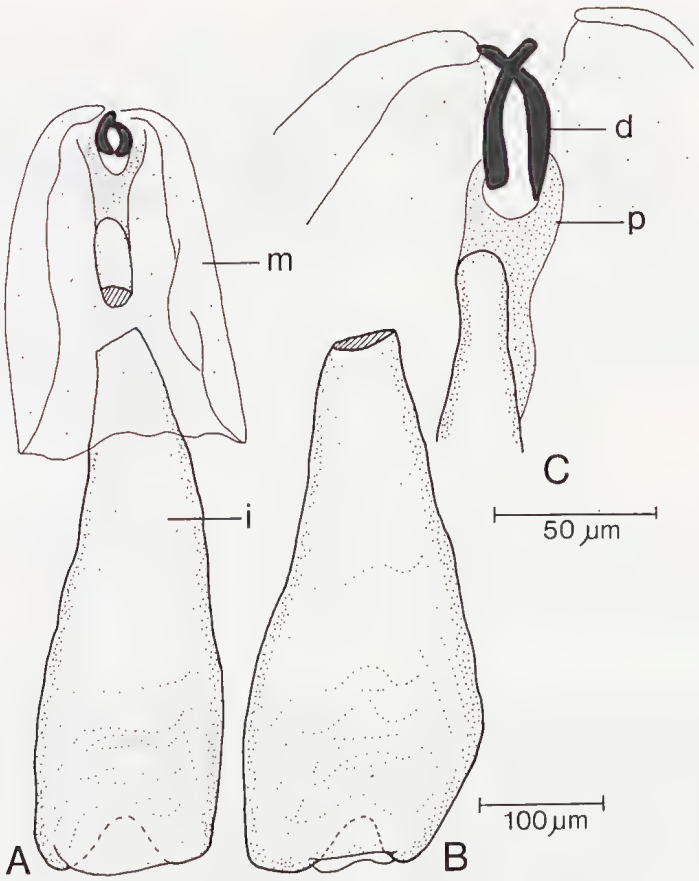

Fig.5. Radula of *Chaetoderma usitatum* n.sp. A, B: paratype no. 1, cone broken; A, posterior view; B, lateral view; C: paratype no. 2 showing detail of lateral projections. d, denticle; i, cone-shaped piece; m, dome-shaped membrane which covers buccal mass; p, lateral projection.

Falcidens Salvini-Plawen, 1969

Falcidens Salvini-Plawen, 1969.
Chaetoderma.-Ivanov, 1981 (non Lovén, 1844). (See Salvini-Plawen, 1984).

Type species. *Falcidens crossotus* Salvini-Plawen, 1984, by original designation.

Diagnosis. With characters of the family. Radula with paired sickle-like teeth attached to the cone-shaped piece (Figs 9, 12, 13).

Distribution. World ocean except Antarctic, especially near coasts.

Falcidens chiastos n.sp.

Figs 2C, 6, 7, 8, 9; Table 1

Type material. HOLOTYPE: Bass Strait, 39°46.0'S, 146°18.0'E, 80 m (RV *Tangaroa*, Stn 159 epibenthic sled, 13 Nov. 1981). MV F54192 (wet specimen, spicule slide. Second spicule slide AM). ILLUSTRATED PARATYPES: Nos 1, 2, 4: type locality. MV F54190 (no.1), F54189 (no. 2) and F54191 (no.4). No. 3: Bass Strait, 39°00'S, 148°24'50"E, 95 m (Esso-Gipps Stn 20, May 1969). AM C156227.

Diagnosis. Translucent and shiny, slender, up to 12 mm long by 0.8 mm diameter, anterior trunk short, narrower than posterior trunk which is about half total body length, anterior constriction not pronounced, posterium less than one quarter body length; spicules mostly flat lying but somewhat erect on anterior trunk and posterium, without distinct waist, ornamented by crossed diagonal ridges, with 25 µm notch or rounded basally, about 50 µm in width, ranging up to 150 µm in length, thickness 8 µm or less; radula length up to 220 µm, cone-shaped piece narrow anteriorly, 10-20 µm, and broad laterally, 60 µm or more, sickle teeth 35 µm, distal ends set widely apart, lateral membranes long, extending one half length of cone.

Etymology. From *chiastos*, arranged diagonally.

Description. *External morphology.* Slender, translucent species up to 12 mm in length (Fig. 6). About 50 percent of body length occupied by posterior trunk containing digestive gland and gonad (range, 38-60 percent, N = 49,

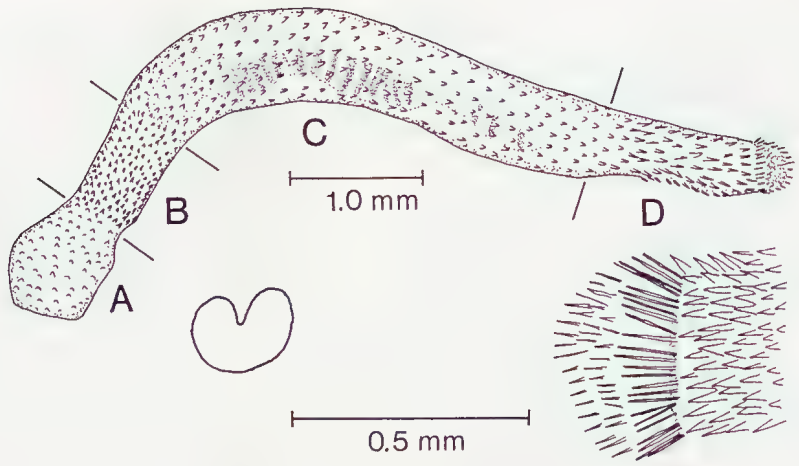

Fig.6. *Falcidens chiastos* n.sp., holotype, entire specimen and cloaca in lateral view, and oral shield of paratype no. 4. Spicules of cloacal region are heavily encrusted, not indicated here. Body divisions are A, neck; B, anterior trunk; C, posterior trunk; and D, posterium.

Stn 159 ES); anterior trunk and posterium short relative to total length, averaging 14 and 23 percent, respectively (ranges, 9-23 percent and 16-30 percent, respectively). Neck about same length as anterior trunk, but of greater diameter (mean diameters 0.6 and 0.4 mm, respectively); constriction between them not pronounced. Long posterior trunk somewhat broader than anterior trunk, averaging 0.6 mm. Narrowest region is the posterium (0.3 mm average).

Spicules on neck and posterior trunk flat lying; internal organs visible, especially dark-coloured stomach and folds of digestive gland. Anterior trunk and posterium opaque, spicules somewhat erect in preserved specimens. Cloaca ringed by short circle of spicules and bears a brush of usually heavily encrusted needles. Dorsoterminal sensory organ not evident.

Oral shield only slightly wider than high and cleft dorsally; withdrawn in most specimens. Dimensions in paratype no. 4 are 0.16 mm in height by 0.21 mm in width; index is 4.20.

Holotype: total length 6.6 mm; neck 0.9 long by 0.7 mm in diameter; anterior trunk 0.8 by 0.5 mm; posterior trunk 3.6 by 0.7 mm; posterium 1.3 by 0.3 mm.

Spicules. Crossed diagonal ridges ornamenting spicules at indistinct waist give species its name (Figs 2C, 7). Most spicules about 50 µm in width, symmetrical and curved slightly toward body; thickest, 6-8 µm, where diagonal ridges cross. Spicules of neck ('b') ovate or widest distally and less than 75 µm in length; those from anterior and posterior trunk ('c'-'f') and posterium ('g') 100-150 µm, at least twice as long as wide. Spicules from neck and trunk rounded distally or rounded with a broad point; those from posterium have a broad point. Proximally, spicules either notched deeply (notch about 25 µm long) or unnotched; neither type predominates. Unnotched spicules either rounded or straight basally. Notch openings vary in width of gap from nearly closed (less than 2 µm) to more than notch width (greater than 10 µm) (Fig. 8). Spicules from region near cloaca ('h') vary from broad and short (50 by 10 µm) with short, sharp distal point to narrow and long (35 µm or less by 125-175 µm) with a long distal point. Needle-like spicules of 150 µm also occur at cloaca.

Radula. Three radulae examined, ranging in total length from 185-220 µm, one quarter to more than one third neck diameter (Fig. 9). Radula in preserved specimens of *Falcidens* oriented with sickle teeth dorsal; largest, and growing, end of cone ventral; and triangular plate faces anteriorly. (Triangular plate probably not attached to sickle teeth as described by Scheltema [1972], but may instead be a guide against which ride the sickle teeth, which are attached to the cone [cf. Fig. 9C and F]). Cone-shaped piece ('i') very narrow anteriorly and posteriorly (12-24 µm) and 3-5 times broader laterally, 60 µm or more at greatest width; cone length in figured paratypes 165 and 185 µm. Sickle teeth ('h') are about 35 µm from base to tip and gape broadly at tips. Entire triangular plate ('c') tanned (i.e., yellowed); has ridges along outer edges (Fig. 9E). Apophyses of triangular plate consist of a bar-shaped piece ('b') and two denticles ('a'). Pair of thin lateral membranes ('y') that lie outside buccal mass about 105 µm long and extend almost half length of cone.

Distribution. *Falcidens chiastos* is the most numerous Chaetodermomorpha species in the Australian samples (Table 1). A total of 199 specimens were examined, all from Bass Strait between 22 and 120 m; sediments ranged from fine muds to fine sands and shell. Densities at some stations were high: 180 m^2 at Stn 156 S-M, 100 m^2 at 181 S-M, and 70 m^2 at 151 S-M.

Closely related species. *Facidens loveni* (Nierstrasz, 1902), described from two complete specimens and a

fragment dredged on the *Siboga* expedition from 1,310 m in the Java Sea (8°0.3'S, 116°59'E, Stn 35), has spicules with similar diagonally crossed ridges (Fig. 7) and a similar body shape. *Falcidens chiastos* differs from *F. loveni* as illustrated by Nierstrasz, however, in having a significantly shorter posterium relative to total length (p less than 0.01 in one population, Stn 159 ES; see Scheltema, 1985, for statistical importance of relative posterium length between species). The spicules of *F. chiastos* are broader relative to their length and more deeply notched than those illustrated for *F. loveni*. The sickle teeth of the radula differ in the two species (Fig. 9); in *F. chiastos*, they have a shorter proximal base and a wider gap between the distal ends than in the illustration for *F. loveni*.

A *Falcidens* species similar to *F. chiastos* occurs beweeen 400 and 600 m on the slope off south-eastern Victoria. A preliminary examination shows it to have longer and narrower spicules with the diagonal ridges incomplete or lacking and with a shallower basal notch.

Two other unnamed species of *Falcidens* with similar notched spicules ornamented by crossed diagonal ridges occurs in the western Atlantic off south-eastern United States and north-eastern South America.

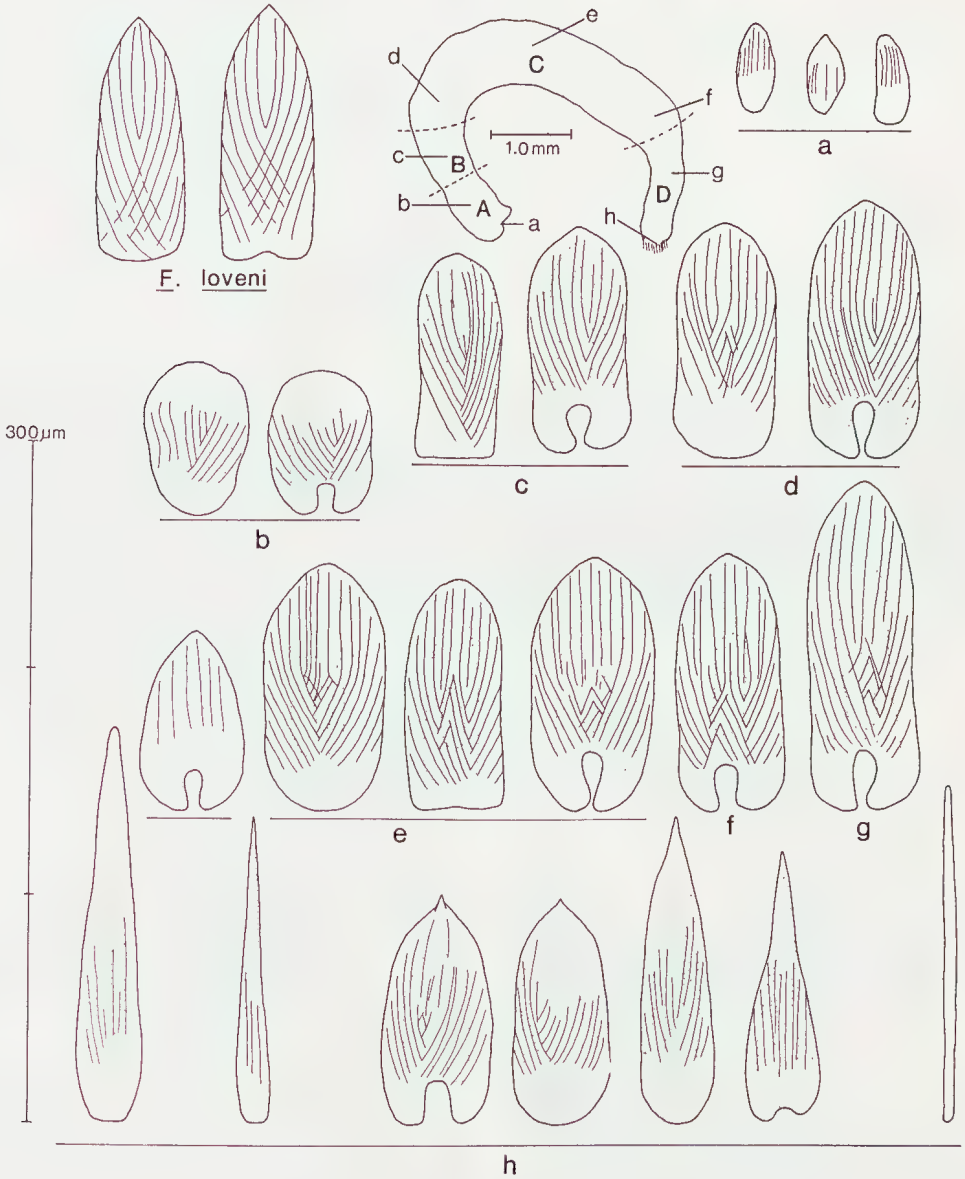

Fig.7. Spicules of *Falcidens loveni* Nierstrasz and *F. chiastos* n.sp. Spicules of *F. loveni* at upper left are redrawn from Nierstrasz (1902, Fig.183) (scale unknown). 'a'-'h', spicules of *F. chiastos* from paratype no. 1 figured at top: 'a', from oral region; 'b', from neck; 'c', from anterior trunk; 'd','e','f', from anterior, midpart, and posterior part of posterior trunk; 'g', from posterium; 'h', from around cloaca. Greatest thicknesses for body regions are: 'a', less than 3 µm; 'b', 6.5 µm; 'c'-'f', 8 µm; 'g', 7.5 µm; 'h', 7 µm.

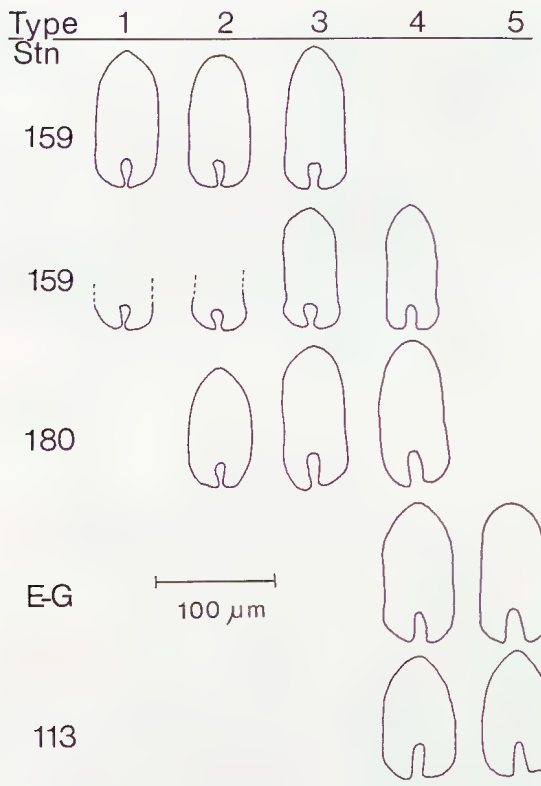

Fig.8. *Falcidens chiastos* spicules, variation in notch width at proximal end of spicule. Spicules in each horizontal row are from the midposterior trunk of a single specimen from the location indicated by station number or letter (see Table 1). Vertical rows show type of spicule notch: 1, nearly closed proximally, opening less than 2 µm; 2, somewhat open, opening 2 to less than 5 µm; 3, width of opening broad but less than greatest notch width, 5-7 µm; 4, notch of even width, sides of notch nearly parallel, opening 8-10 µm; 5, notch widest at opening, greater than 10 µm.

Falcidens lipuros n.sp.

Figs 2D, 10, 11, 12; Table 1

Type material. HOLOTYPE: Bass Strait, 38°57.8'S, 148°26.5'E, 130 m (RV *Tangaroa*, Stn 170 Smith-McIntyre grab, 15 Nov 1981). MV F54188 (wet specimen, spicule slide. Second spicule slide AM). ILLUSTRATED PARATYPE: No. 1: type locality. MV F54187.

Diagnosis. Short, thick body up to 6.7 mm long, broadest at anterior trunk (up to 1.0 mm in diameter), tapered posteriorly, posterium short and not tail like, posterior trunk more than half total body length, anterior constriction narrow but distinct; trunk spicules flat lying, elongate, up to 200 µm long and 50 µm wide, less than 8 µm thick, notched or rounded basally, many with broad ridges at waist not parallel to edges or medial axis, waist usually distinct, blade pointed distally; radula 200 µm long, cone narrow anteriorly, 15 µm, and broad laterally, 60 µm, sickle teeth 48 µm with points nearly meeting, lateral membranes short, extending less than one quarter length of cone.

Etymology. From *lipuros*, without a tail.

Description. *External morphology.* Short, anteriorly broad species without distinct tail, or posterium (Fig. 10). Greatest length of 3 known specimens 6.7 mm. Anterior trunk short, only one sixth total length, and broadest part of body, up to 1.0 mm in diameter. Neck short, one tenth body length, 0.1-0.2 mm narrower than anterior trunk; very narrow but distinct constriction appears as fine line between them. Posterior trunk more than half total length; tapers gradually to posterium, narrowing to 0.1 or 0.2 mm less in diameter than anterior trunk. Short posterium, one sixth total length, is relatively broad, 0.4-0.5 mm in diameter. Anterior and posterior ends of body flat when contracted. Dorsoterminal sensory organ evident. Oral shield of paratype no. 1 twice as wide laterally as high (0.27 by 0.14 mm), with deep dorsal cleft extending more than halfway ventrally; index is 4.72.

Spicules flat lying and distinctly pointed; increase in length posteriorly. Posterior trunk translucent, dark digestive gland apparent. Cloaca encircled by a ring of spicules shorter than those of posterium; spicules of contracted posterior wall converge like spokes of a wheel into center.

Holotype: total length, 6.8 mm; neck 0.8 long by 0.8 mm diameter; anterior trunk 0.9 mm by 1.0 mm; posterior trunk 4.2 by 0.9-0.8 mm posteriorly; posterium 0.9 by 0.5 mm.

Spicules. Spicules of *F. lipuros* symmetrical, flat and either notched or rounded basally (Figs 2D, 11). Side edges of both base and blade convex; waist usually distinct (but indistinct in Fig. 2D); many, but not all, spicules have distinct, wide, longitudinal grooves and ridges at waist not parallel to sides or to medial axis. Thickest part of spicules is medial and extends from base to just beyond waist; greatest thickness (up to 8 µm) same in neck and trunk spicules. Blade broad relative to base. Distal tips thin and often broken off.

Spicules from oral region ('a') thin (up to 4 µm), elongate (up to 60 µm long by 20 µm wide), often somewhat pointed, without ridges. Spicules of neck ('b') and anterior trunk ('c') have broad blade with distinctly convex edges, end in a nipple-like point distally. Blades and bases about equal in length; total lengths and base widths range up to 100 by 42 µm on the neck and up to 120 by 50 µm on anterior trunk.

Blades in spicules of posterior trunk ('d', 'e') longer than bases, have only slightly convex edges, ending in a point not set off from rest of blade. Spicule lengths and base widths range up to 180 by 50 µm anteriorly and up to 200 by 55 µm posteriorly.

Spicules of posterium ('f') have elongate, narrow blades and range up to 350 µm in length, 50 µm in width, and 10 µm in thickness; interspersed are spicules like those of trunk.

Scattered on neck and trunk are few thin (4-5 µm), short,

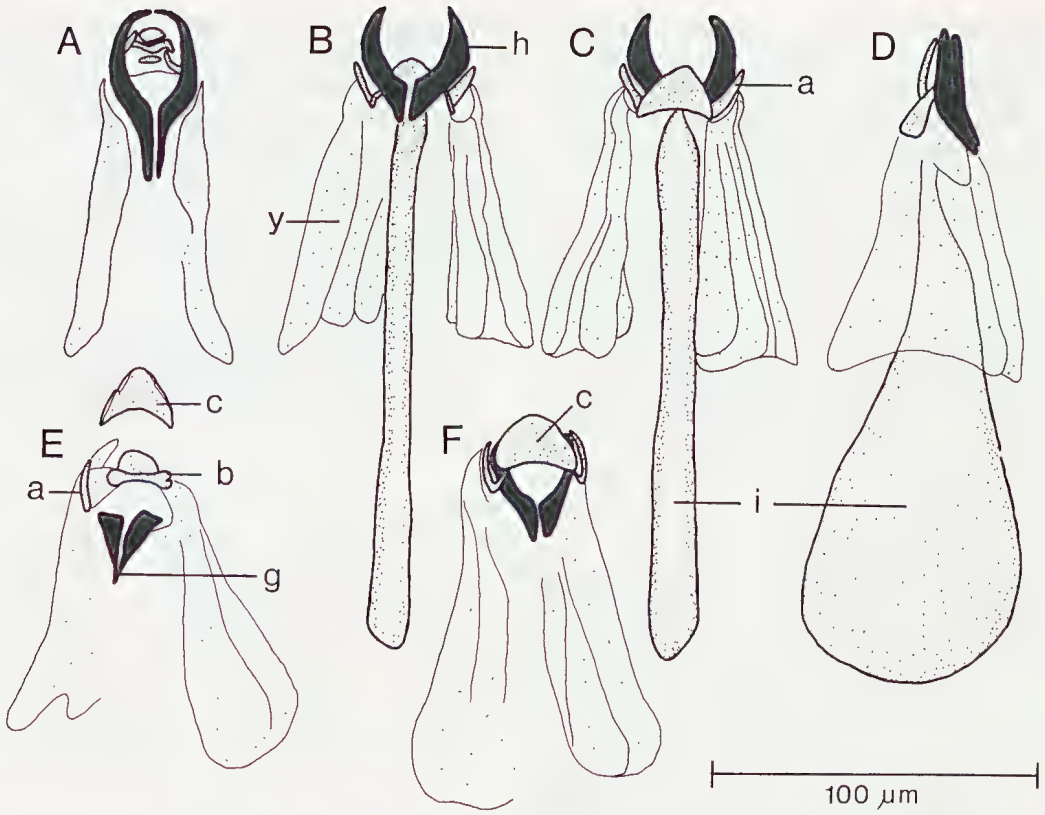

Fig.9. Radula of *Falcidens loveni* (Nierstrasz) (A) and *F. chiastos* n.sp. (B-F). A: redrawn from Nierstrasz (1902, fig.191); B-D: paratype no. 1, posterior (B), anterior (C), and lateral (D) views; E: paratype no. 2; F: paratype no. 3. In E, the triangular plate 'c' has broken away from its apophyses 'a' and 'b' and shows ridged edges; the sickle teeth 'h' are broken off, but the proximal spring connection 'g' remains. In F the triangular plate 'c' is more distal relative to the sickle teeth than in the radula drawn in B and C, probably indicating preservation at different times of radula movement. a, b, apophyses of triangular plate; c, triangular plate; g, spring-like connection of sickle teeth; h, sickle teeth; i, cone-shaped piece; y, lateral membranes that lie outside buccal mass. Scale applies to B-F; unknown for A.

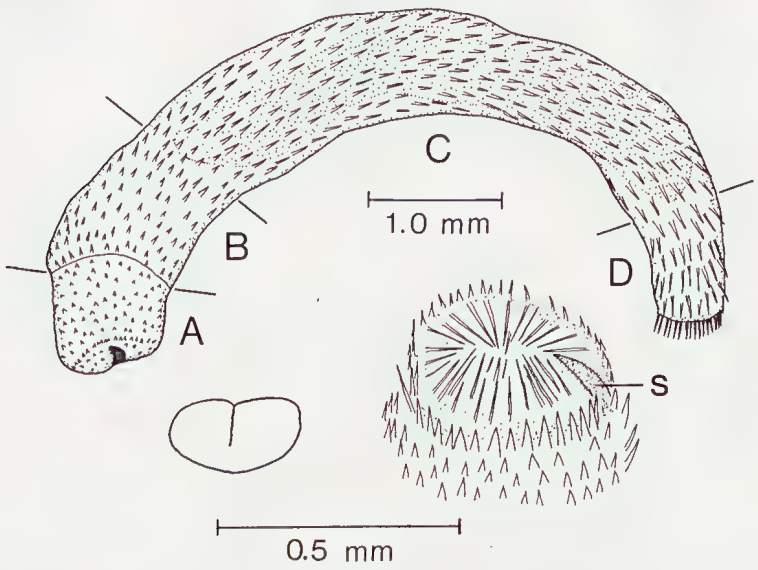

Fig.10. *Falcidens lipuros* n.sp., holotype, entire specimen and posterolateral view of cloaca, and oral shield of paratype no. 1. Body divisions are A, neck; B, anterior trunk; C, posterior trunk; and D, posterium. The dorsoterminal sensory organ ('s') is evident.

subtriangular spicules posteriorly ('e') having a long, narrow, thickened blade.

Spines surrounding cloaca are less than 300 µm long and 8 µm thick, shorter and thinner than longest posterium spicules; base flattened and narrow, 15 µm in width.

Radula. One radula examined (Fig. 12); total length 200 µm, nearly one third neck diameter. Cone-shaped piece 155 µm long and anteriorly and posteriorly very narrow (15 µm), one quarter lateral width (60 µm). (See description above of *F. chiastos* radula and Fig. 9 for radula morphology.) Sickle teeth 48 µm from base to tip; tips curve towards each other nearly to touch. Tanned portion of triangular plate shaped like inverted base of heart and bears on each side a broad, tanned apophysis extending only slightly onto sickle tooth. Connections to second pair of denticles lying alongside sickle teeth were not seen. Lateral membranes short, about 70 µm in length, extend less than one quarter length of cone.

Distribution. Three specimens were taken from two stations at 120 and 130 m with mixed mud and sand in Bass Strait (Table 1).

Closely related species. *Falcidens lipuros* and *F. chiastos* may at first be confused when they are found in the same sample, but the greater anterior trunk width and longer posterior spicules in *F. lipuros* quickly distinguish them

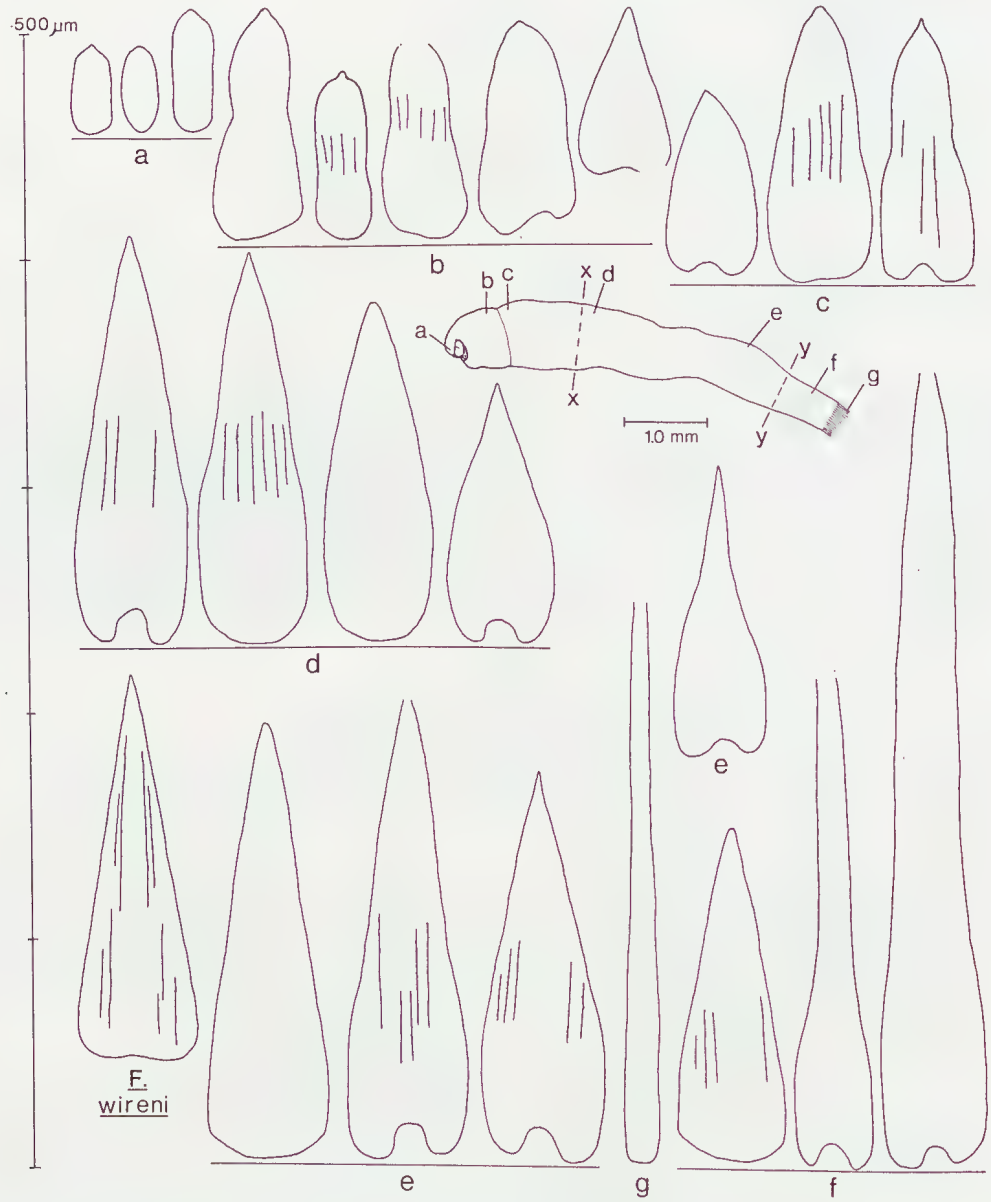

Fig.11. Spicules of *Falcidens lipuros* n.sp. and *F. wireni* (Nierstrasz) (redrawn from Nierstrasz, 1902, fig.205, scale unknown). 'a'-'g', spicules from paratype no. 1 figured at upper right: 'a', from oral region; 'b', from neck; 'c', from anterior trunk; 'd','e', from anterior and posterior part of posterior trunk; 'f', from posterium; 'g' from around cloaca. Line x-x, division between anterior and posterior trunk; y-y, division between posterior trunk and posterium. Greatest thicknesses for body regions are: 'a', 4 µm; 'b'-'e', 7.5-8 µm; 'f', 10 µm; 'g', 8 µm.

under a dissecting microscope. Under a compound microscope, the spicules are distinctive.

Falcidens wireni is a species 11 mm long described by Nierstrasz (1902) from 1,570 m in the Banda Sea at 4°24.3'S, 129°49.3'E; from Nierstrasz's drawings (fig. 204) and description it is similar to *F. lipuros* in being wider anteriorly (more than 1 mm) than posteriorly (1 mm), in lacking a tail-like posterium, and in having a flat, blunt anterior end. The illustrated spicule of *F. wireni* (fig. 205A; redrawn here, Fig. 11) is somewhat like those of *F. lipuros* in general proportions of length to width and in having longitudinal ridges; however, the sides are straight rather than convex and the ridges are not restricted to the region of the waist. The radula drawings are inadequate for comparison.

A species of *Falcidens* similar to *F. lipuros* occurs on the slope off south-east Victoria between 363 and 800 m. Cursory examination shows it to have spicules that are shorter and keeled with fine parallel ridges extending far distally on the blade.

Falcidens macrafrondis n.sp.

Figs 2E, 13, 14; Table 1

Type material. HOLOTYPE: off Wollongong, NSW, 34°27-26'S, 151°27'E, 1200 m. AM C156228 (wet specimen, spicule slide. Second spicule slide MV F54193). PARATYPE: type locality. AM C156229.

Diagnosis. Small for genus, less than 4.5 mm long by 0.5 greatest diameter, posterium probably elongate and narrow; trunk spicules triangular, very large and thick for body size, more than 300 μm in length and 150 μm in base width, 10 μm or more thick, distally pointed, blade with numerous sharp longitudinal ridges and broad keel, waist not distinct; radula cone short (60 μm) relative to tooth length (45 μm), total length (100 μm) about one fifth neck diameter.

Etymology. From *macra,* large and *frons,* leaf.

Description. *External morphology.* Two specimens collected have been distorted by stretching and length of body divisions cannot be determined (Fig. 13). Total stretched length about 4.5 mm; width of neck, which is not stretched, about 0.5 mm. Posterium presumably elongate, body-wall musculature weak. Probably no anterior constriction between neck and anterior trunk. Paratype female, as determined in glycerine-squashed preparation, with largest egg 32 by 45 μm, size possibly indicates immature specimen of average adult body length (see Scheltema, 1987). Spicules remarkably large for body size, even in oral area; spicules project from neck and withdrawn mouth, but presumably flat lying on trunk, although most trunk spicules lost from specimens. Ring of long spicules surrounds relatively large, rounded cloaca (0.4 long by 0.3 mm wide); tips of spicules broken off in holotype. Shape of oral shield not known; dorsoterminal sensory organ not evident.

Spicules. Spicules flat and range in size from about 200 to 350 μm in length (Fig. 14) with broad base 70 to 150 μm

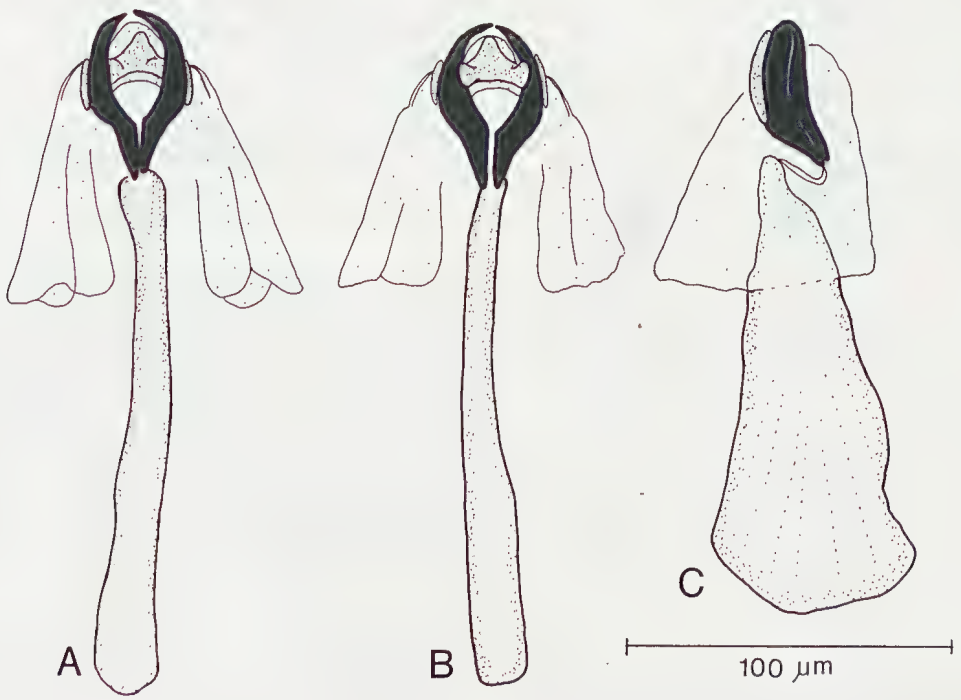

Fig.12. Radula of *Falcidens lipuros* n.sp., paratype no. 1. A, B, C: posterior, anterior, and lateral views, respectively (cf. Fig. 9). Lateral view somewhat tilted and foreshortened.

wide; those that ring cloaca 30 μm in width. Spicules from most anterior end large, especially those ventral to mouth (120 μm long). Blades have broad keel and numerous fine, sharp, longitudinal ridges that run fan like, converging distally (Fig. 2E). Waist not distinct. Spicules are thickest at keel, 10 μm or more; entire spicule flat and thick, 7 μm over its greater area in spicules 200 μm long, and 9 to 10 μm in spicules 350 μm long. Distal end sharply pointed; edges often becoming concave in outline near tip. Proximal end of base straight or somewhat indented.

Radula. Radula small, 100 μm in total length (Fig. 13) and about one fifth neck diameter. Cone only 60 μm long, hardly longer than sickle teeth, which are 45 μm long; such a short cone may indicate early growth in immature specimen. Anterior cone width 15 μm; lateral width, 38 μm, about 2.5 times greater. Triangular plate approaches bar shape; has 3 distinct little denticles that bend towards sickle teeth. Apophyses consist of pair of denticles. Lateral membranes short, about 35 μm, extend down only one tenth length of cone.

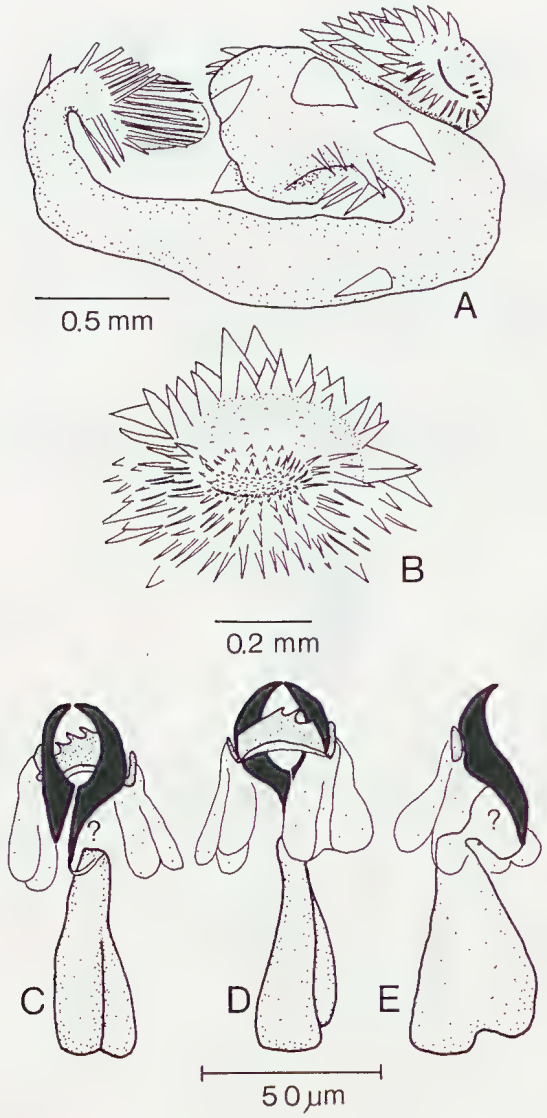

Fig.13. *Falcidens macrafrondis* n.sp., holotype (A,B) and radula of paratype (C-E). Spicules illustrated on the trunk of the holotype (A) are the only ones remaining in this view; spicules ringing the cloaca are broken. C, D, E: posterior, anterior, and lateral views, respectively (cf. Fig. 9).

Distribution. Only two specimens from 1200 m off Wollongong, New South Wales, are known (Table 1).

Closely related species. There are no known species close to *F. macrafrondis* with its large spicule size relative to body size.

Falcidens spp.

A single specimen of a species with a long posterium was collected from Bass Strait at 1,120 m (Stn Q631, Table 1).

Prochaetodermatidae Salvini-Plawen, 1969

Diagnosis. Chaetodermomorpha with large, cuticular jaws and small, distichous radula with 8-13 rows of paired teeth on unipartite radular membrane; each tooth with medial serrated membranous brush and lateral wing (Fig. 17D), radular membrane with tooth-like projections that extend along each tooth (Fig. 17B). Oral shield divided, often bordered by large spicules; posterium usually tail like; trunk not divided (Fig. 15); dorsoterminal sensory organ present but not evident (Haszprunar, 1987). Genera differentiated on basis of nonoverlapping character states of spicules shared by several species, some still undescribed (Scheltema, 1985).

Rhabdoderma n.gen.

Type species. *Rhabdoderma australe* n.sp.

Diagnosis. With characters of the family. Spicules rod like, symmetrical or somewhat asymmetrical, long, thick, pointed, flattened, lacking obvious ornamentation; base longer than blade on trunk spicules (Figs 2F, 16). Spicules of trunk bound to body and arranged obliquely; they diverge on each side of ventral midline, spiral up dorsally and posteriorly, and meet at angle along dorsal midline (Fig. 15). Differentiated from *Chevroderma* Scheltema, 1985 by lack of longitudinal groove and chevron-shaped cross grooves on spicules.

Distribution (based largely on undescribed species). Off south-eastern Australia; north-eastern Pacific; western Atlantic from south of Cape Hatteras to the Argentine Basin; eastern Atlantic from West European Basin to Namibia Basin.

Etymology. From *rhabdos*, a rod.

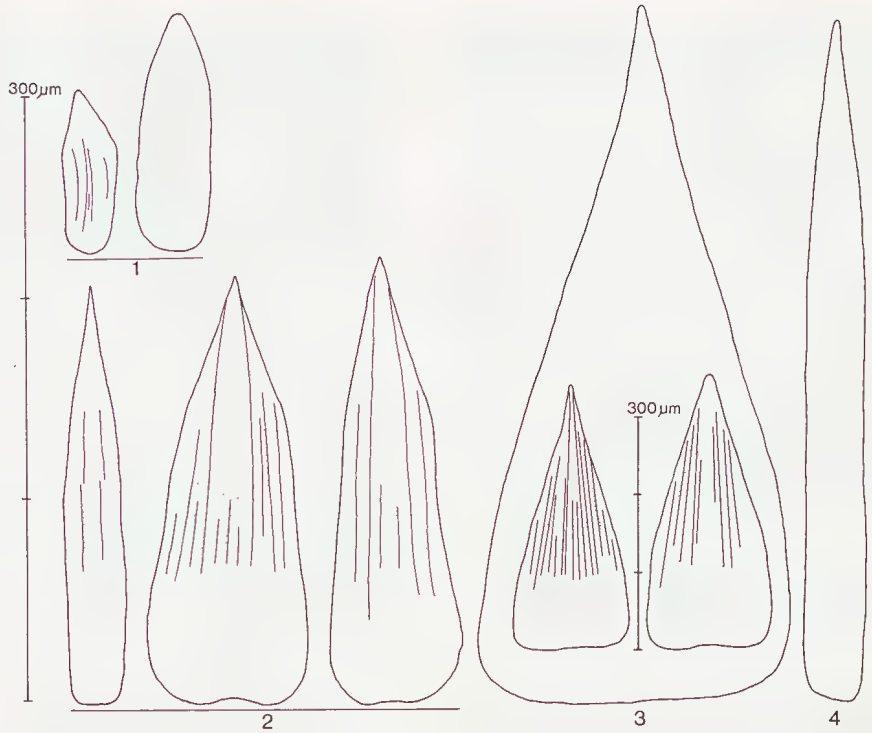

Fig.14. Spicules of *Falcidens macrafrondis*, paratype: 1, probably from anteriormost end; 2 and 3, trunk spicules, but spicule on left perhaps from posterium; 4, one of the spicules ringing the cloaca, drawn from glycerine-squashed preparation. In 3, large spicule in outline is at the same magnification as spicules labeled 2; spicules within the outline are the same size as the outline but drawn at less magnification. Greatest thicknesses are: 1, 9 µm; 2, 3, greater than 10 µm; 4, not determined.

Rhabdoderma australe n.sp.

Figs 2F, 15, 16, 17; Table 1

Type material. HOLOTYPE: off Wollongong, NSW, 34°27'-26'S, 151°27'E, 1,200 m. AM C156230 (wet specimen, spicule slide. Second spicule slide, MV F54196). DESCRIBED PARATYPES: No. 1: type locality. AM C156231. No. 2: Bass Strait, 38°55.6'S, 148°46.4'E, 1,730 m (RV *Tangaroa*, Stn Q635, pipe dredge, 16 Nov. 1981). MV F54195.

Diagnosis. Large and broad prochaetodermatid, largest specimens more than 5 mm long by 1 mm in trunk diameter; posterium about one third total length; trunk translucent, spicules up to 400 µm long, narrow (less than 50 µm), and thick (10 µm or more), crossing at acute angle mid-dorsally, ornamented with fine striations, blade short relative to base, waist indistinct or lacking, base usually tapered; cloaca conical, spicules not in distinct ring; oral shield spicules not obviously larger than surrounding spicules; teeth of radula and jaws large, 175 and 825 µm long, respectively, central plate D-shaped, 45 x 18 µm.

Description. *External morphology. Rhabdoderma australe* is large for a prochaetodermatid both in length (up to 5.2 mm) and in trunk diameter (up to 1.1 mm) (Fig. 15). Posterium one third to two fifths body length and about one half body width. Trunk translucent; spicules closely bound to body and meet at a pronounced angle mid-dorsally. Spicules of anterior end large and stand out somewhat from body; on opaque posterium spicules extend away from body. Oral shield spicules not obviously larger than surrounding spicules; oral shield does not cover entire oral area of anterium in some specimens. Cloaca conical and not surrounded by discrete ring of spicules; spicules of cloaca brush like.

Holotype: total length 4.8 mm; trunk 2.9 by 1.1 mm; posterium 1.9 by 0.5 mm; index of posterium length to trunk length 0.66. Oral shield (left half of pair) 0.13 by 0.20 mm, index 2.36.

Spicules. Spicules long, thick, curved slightly toward body (Fig. 16); numerous faint striations run lengthwise (Fig. 2F). Base longer than blade except in a few spicules from anterior end ('a') and in those from posterium ('d'). Sides of base gently convex; in some spicules convexity greater on one side than the other and spicules slightly asymmetrical (cf. genus *Chevroderma* Scheltema, 1985). Proximal end of base rounded and either tapered or untapered, or straight and either untapered or flared. Short blade has rounded point distally; side edges either continue curve of base or set off by slight indentation at waist. Spicules thickest medially; isochromes symmetrical.

At anterior end (region 'a') spicules long (up to 160 µm), thick (7-10 µm), and up to 40 µm wide; distal ends of blade bluntly rounded and waist usually distinct.

Most spicules from lateral and dorsal trunk (regions 'b_1' and 'c_1') are 300 to nearly 400 µm long, 35-45 µm wide, and 9 to more than 10 µm thick, but spicules from ventral

body surface ('b_2' and 'c_2') are smaller, less than 200 µm long, 25-30 µm wide, and 5 to 8 µm thick, with usually sharper distal points. Scattered amongst most usual spicules are other types: (1) short (length 160 µm), thin (7 µm), blade narrow and sharply pointed with distinct waist; (2) long (up to 350 µm), thick (greater than 10 µm), with edges of sides parallel and 9-µm isochromes running parallel to each other to straight proximal end of base, waist not distinct; (3) similar to type (2) except shorter (80-160 µm long) and with flared base; (4) short (225 µm in length) and broad (45 µm width) with a broad blade. Some specimens have many type 2 spicules, and some have few.

Spicules of posterium (region 'd') long and narrow, from 350 µm up to 425 µm long and 30 µm or less in width. Blades longer and thicker (up to 10 µm) than base which is scarcely or not at all tapered.

Spicules from cloaca (region 'e') narrow, curved rods 10 µm thick and somewhat more pointed distally than proximally; same length (up to 425 µm) as those from posterium.

Radula. Radula and jaws in *F. australe* large; teeth in 12-13 rows, first 3 pairs worn. In a specimen with trunk measuring 3.0 by 1.1 mm (paratype no. 1), teeth 175 µm long with broad lateral wing (Fig. 17). Jaws 825 µm long by 390 µm wide. Membranous lateral tooth-like extensions of radular membrane large and obvious, reaching half way up sides of teeth with small basal projection. Central plates D-shaped, thin and indistinct, of average length (45-50 µm) for family, but wide, up to 18 µm. In much smaller specimen (trunk 1.6 by 0.6 mm), teeth 130 um long, jaws 560 by 280 µm, central plates 40 by 18 µm.

Distribution. A total of 69 specimens were taken from the slope between 1,120 and 2,510 m off Wollongong, New South Wales, and Point Hicks, Victoria (Table 1).

Prochaetoderma Thiele, 1902

Type species. *Chaetoderma raduliferum* Kowalevsky, 1901 by monotypy.

Diagnosis. With characters of the family. Spicules flat; base shorter than blade, blade triangular with median keel and sharp distal point; waist present (Fig. 1B).

Distribution. Eastern and western Atlantic Ocean; Mediterranean; off south-eastern Australia.

Prochaetoderma sp.

Fig. 1B

A single small specimen 1.9 mm long with a very short posterium (0.19 x trunk length) was taken from 1,120 m in

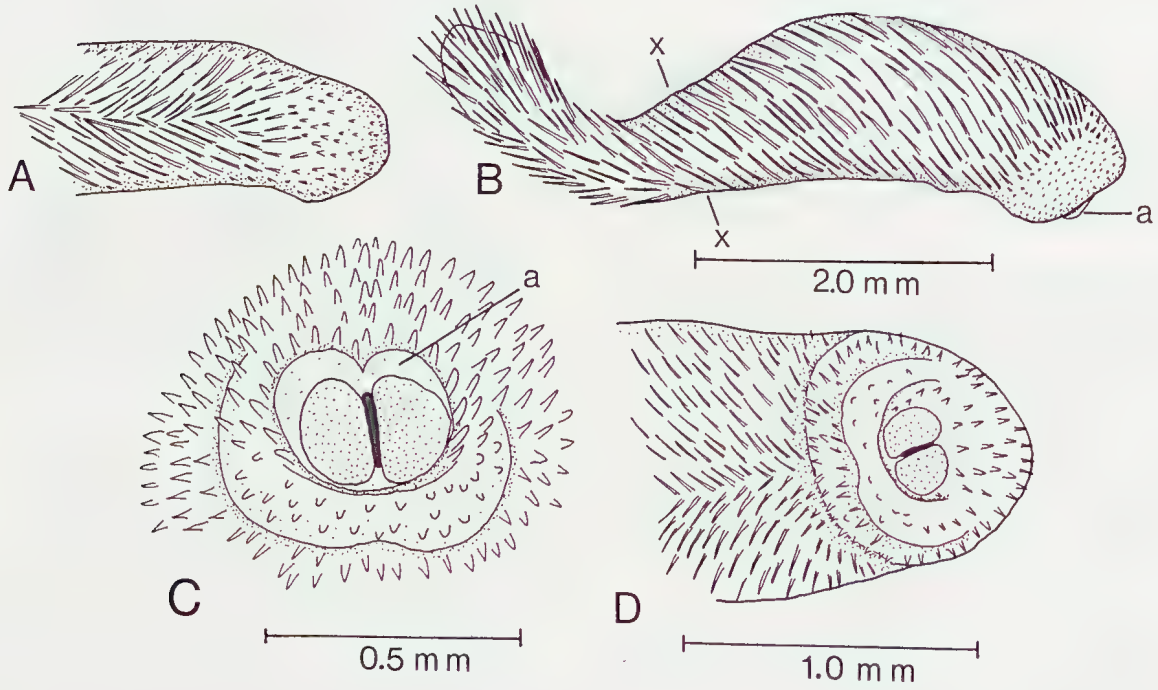

Fig.15. *Rhabdoderma australe* n.sp., holotype. A: anterodorsal view; B: lateral view; C: anterior view, oral shield and anterium; D: anteroventral view. a, anterium; x-x, division between trunk and posterium. A and B at same scale.

the same sample as a specimen of *R. australe* (Stn Q631, Table 1). The spicules are long for the size of the specimen, up to 300 µm, a condition often seen in juveniles, whose spicules usually appear to be too large for them. However, eggs measured through the integument are nearly 100 µm long, a size which indicates adult body length but not full maturity (see Scheltema, 1987).

The genus has not been recorded before from the Pacific. (*Prochaetoderma californicum* Schwabl belongs to the genus *Spathoderma;* determination based on re-examination of syntypes, not yet published.) A full description and species designation awaits additional specimens. [New material from Slope Stn 27 provides 4 specimens (Table 1).]

Undetermined Prochaetodermatidae

A single specimen of a prochaetodermatid species lacking spicules was taken from 55 m in Bass Strait at R.V. *Hai-kung* Stn 139 (Table 1). It is not the same as either of the above species.

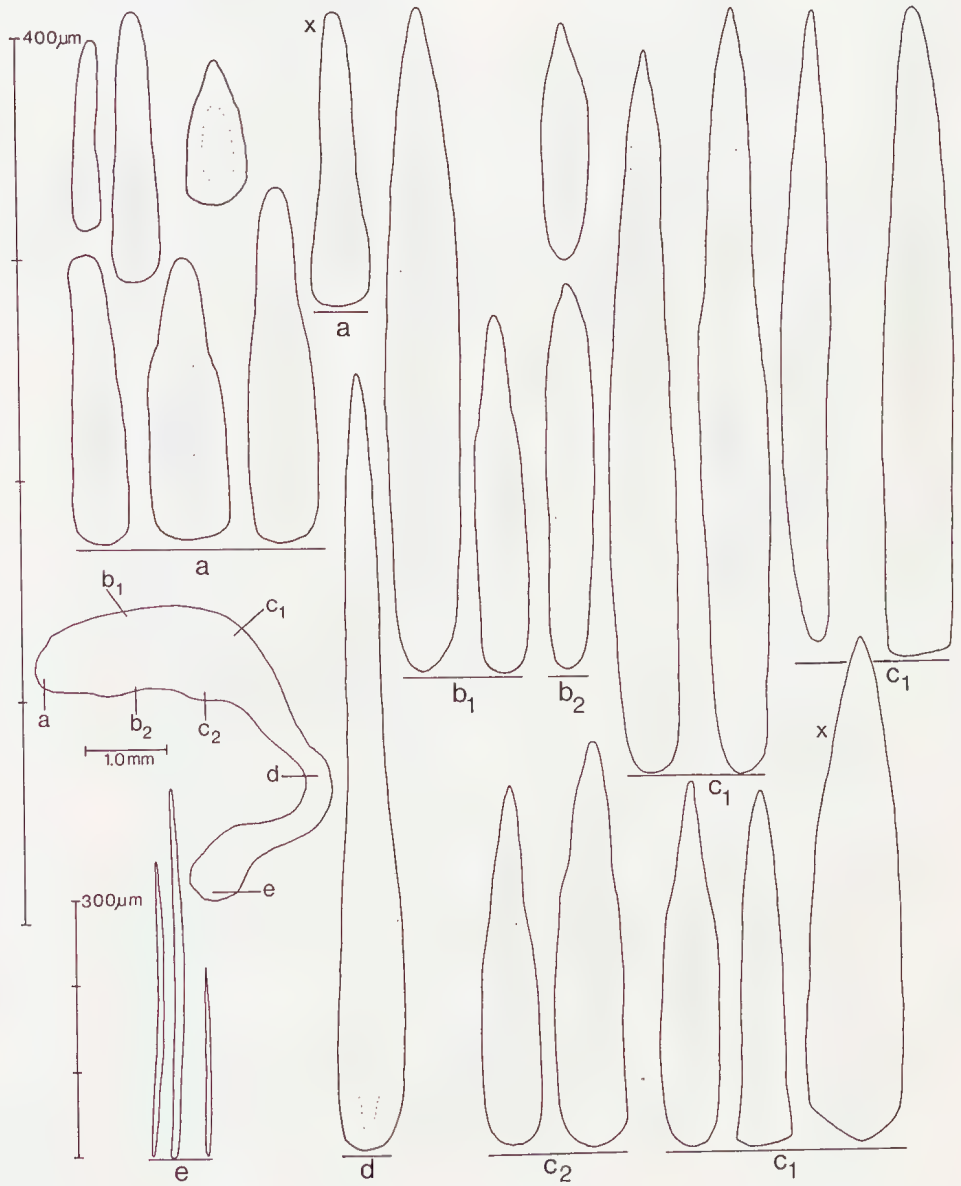

Fig.16. Spicules of *Rhabdoderma australe* n.sp. Spicules are from body regions 'a'-'e' of paratype no. 1 as indicated in figure, except for two marked x, which are from other specimens. Thickest spicules from each body region are 10 µm or more thick, except for ventral spicules b_2 and c_2, which are up to 7 and 8 µm thick, respectively. Ornamentation of fine lengthwise striations (see Fig. 2F) is not shown. The posterium of paratype no. 1 is unnaturally stretched.

Undetermined Chaetodermomorpha

A single specimen of a small (2.5 mm), transparent chaetodermatid with thin spicules thinly dispersed and deeply imbedded in the cuticle was taken from 56 m at Stn T-163 S-M (Table 1).

Undetermined slope species

Besides the species listed in Table 1, the following new slope species have been recently received and await description: three species of *Falcidens*, two species of *Chaetoderma*, one species of *Scutopus*, and one species of *Limifossor*. The recorded ranges of *Scutopus* and *Limifossor* are thus extended to the western Pacific.

Discussion

The aplacophoran fauna of the Pacific is not well known.

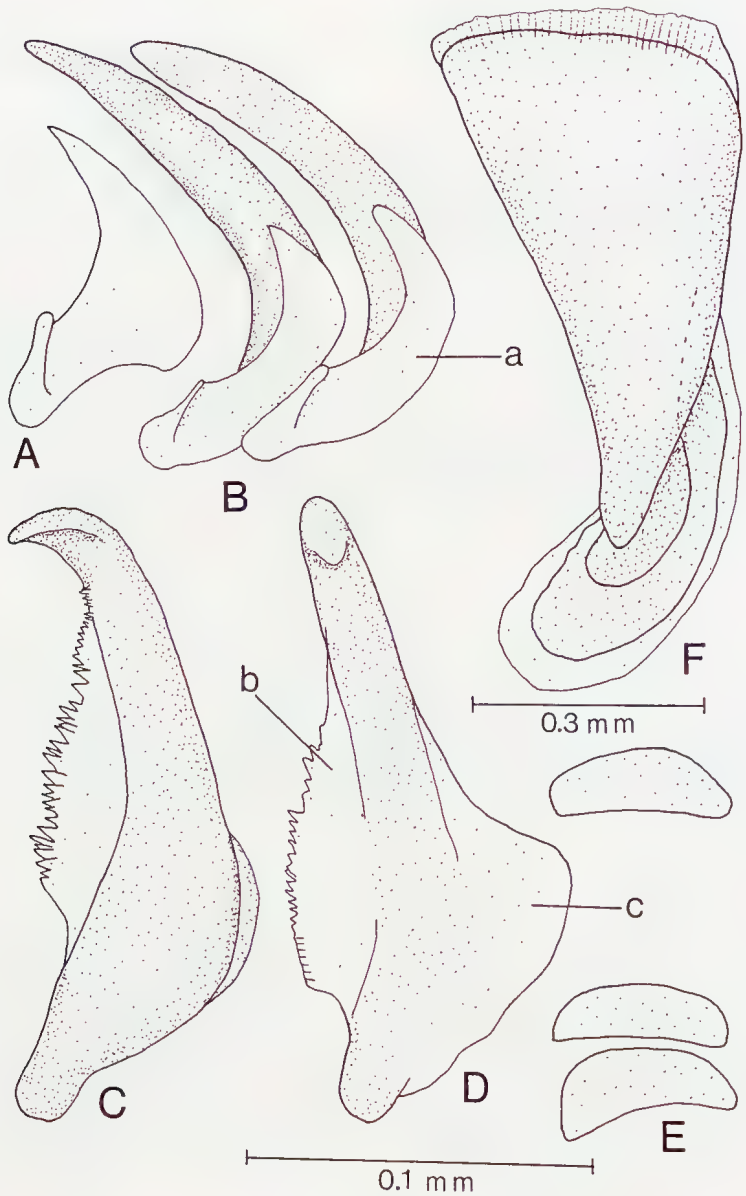

Fig.17. Radula and jaw of *Rhabdoderma australe* n.sp., paratype no. 1. A: lateral tooth-like extension of radular membrane; B: third and fourth teeth from proximal end of radular sac, lateral view, anterior to right; lateral tooth-like extensions ('a') in natural position; C, D: two views of individual teeth showing medial denticulate membrane, or brush ('b'), and lateral wing ('c') (bent over in view C); E: central plates; F: left jaw, lateral view from inside; mouth opens at right.

Most of the species of Pacific Chaetodermomorpha that have previously been described were collected by four surveys: the *Siboga* Expedition (Nierstrasz, 1902; Stork, 1941), the U.S. Fish Commission vessel *Albatross* (Heath, 1911), the Pacific Expedition of the Allan Hancock Foundation, University of Southern California (Schwabl, 1963), and the USSR Academy of Sciences in the Sea of Japan (Ivanov, 1984). The great *Challenger* Expedition collected only one aplacophoran in the Pacific (Selenka, 1885). Several additional descriptions not part of surveys or expedition reports have also been published (Okuda, 1943; Salvini-Plawen, 1972; Osorio & Tarifeño, 1976; Scheltema, 1985). The total number of Chaetodermomorpha species so far described is small, about 36 (Table 2). Some of this number are suspected to be synonyms; species names known to be synonyms from examination of new material and re-examination of types are reflected in the table numbers.

The 16 new species collected off south-east Australia increase the number of Pacific Chaetodermomorpha by a half. The vertical distributions of these species by genus are similar to those of previously described species, with the exception of the genus *Chaetoderma* (Table 2). *Chaetoderma* is not represented at all in the south-east Australian shelf collections, and only by one species on the upper slope, whereas in the rest of the Pacific, species of *Chaetoderma* occur mostly at depths less than 1,000 m. Furthermore, in the family Chaetodermatidae, the genus *Falcidens* off south-east Australia, unlike the rest of the Pacific, has more species than the genus *Chaetoderma*. This preponderance of *Falcidens* species perhaps reflects speciation in that region.

Two species of Chaetodermomorpha off south-east Australia are common. *Falcidens chiastos* occurs at densities up to 180 m^2 in 20 of the 46 shelf samples that contain Aplacophora. The slope prochaetodermatid species *Rhabdoderma australe* also appears to be abundant at depths below 1,000 m, although quantitative data are lacking (Table 1). Some members of the Prochaetodermatidae are known to be among the most numerically abundant animals in the deep-sea fauna, including a Pacific species in the closely related genus *Chevroderma* (Scheltema, 1985).

The genus *Psilodens* Salvini-Plawen, 1977 (= *Scutopus partem*) does not occur in the shelf or slope samples, although it is in collections from both the east Pacific and Indian Ocean (the latter is unpublished). An uncommon but widespread genus, it probably will eventually be found

Table 2. Distribution of Chaetodermomorpha in the Pacific by depth.

Genus	Depth m[1]	Previously Described[2] No. Species	New spp. off South-east Australia No. Species	Total Species
Scutopus	<200	0	0	0
	200-1,000	1	1	2
	>1,000	0	0	0
Psilodens	<200	0	0	0
	200-1,000	0	0	0
	>1,000	1	0	1
Limifossor	<200	0	0	0
	200-1,000	2	1	3
	>1,000	0	0	0
Falcidens	<200	1	2	3
	200-1,000	1	3	4
	>1,000	3	2	5
Chaetoderma	<200	4	0	4
	200-1,000	18	1	19
	>1,000	3	2	5
Prochaeto-dermatidae (genera combined)	<200	0	1	1
	200-1,000	1	0	1
	>1,000	1	2	3
TOTAL		36	15[3]	51

[1] <200 m - shelf species; 200-1,000 m - upper slope species, including those that also extend onto the shelf; >1,000 m - lower slope or abyssal species, including those that also extend onto the upper slope or, in a few cases, also onto the shelf. [2] Numbers reflect known, but unpublished, synonyms. Data from Heath (1911), Ivanov (1984), Nierstrasz (1902), Okuda (1943), Osorio & Tarifeño (1976), Salvini-Plawen (1972), Scheltema (1985), Schwabl (1963), Selenka (1885), and Stork (1941). [3] A single specimen of a shelf species of undetermined affinity is not included (Stn 163 S-M, Table 1).

off the Australian coast.

ACKNOWLEDGEMENTS. Drs C.C. Lu of the Museum of Victoria and Winston F. Ponder of the Australian Museum, Sydney, kindly lent me the aplacophorans in the collections of their museums. The impetus for describing the collections comes from the upcoming publication of the *Fauna of Australia*, which would otherwise have a rather scanty chapter on *Aplacophora*. Susan Houghton took the scanning electron microscope photographs. Contribution no. 6762 from the Woods Hole Oceanographic Institution.

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Amphipoda from the South Pacific: the Society Islands

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Abstract. Thirty two species of gammaridean Amphipoda are recorded from 0 to 1 m depth in the Society Islands. Six species in the genera *Elasmopus, Maera, Cheiriphotis, Polynesoecetes* n.gen. and *Jassa* are new to science and are described and figured.Based on the shallow-water Amphipoda, the Society Islands show their closest biogeographic relationship with Tonga, Fiji and New Caledonia to the west.

Myers, A.A., 1989. Amphipoda from the South Pacific: the Society Islands. Records of the Australian Museum 41(1): 63-82.

Collections of gammaridean Amphipoda (0 to 1 m depth) were made by the writer in 1986, at the Society Islands of Tahiti, Moorea (Windward Islands), Huahine and Bora Bora (Leeward Islands) and are reported on here. There appear to be no previous published records of marine amphipods from these islands, but a terrestrial species, *Talorchestia rectimana* (Dana) is known from the interior of Tahiti. Pacific islands, atolls or archipelagos from which amphipods have been described include: Caroline Islands (Barnard, 1965), Fiji (Myers, 1985c), Gambier and Tuamotu (Chevreux, 1908), Hawaii (Barnard, 1970), Kapingamarangi (Barnard, 1965), Kiribati and Tuvalu (Schellenberg, 1938), Marshall Islands (Schellenberg, 1938, Barnard, 1965), New Caledonia (Ledoyer, 1984), Niue (Myers, 1986a), and Tonga (Myers, 1986b).

Present work revealed a low biomass of marine amphipods in the Society Islands when compared with other well studied Pacific Islands. This was also noted by Ledoyer (personal communication). Chevreux (1908) reported low amphipod density in the Gambier and Tuamotu archipelagos. Myers (1985c) recorded amphipod densities of over 4,000 m^{-2} in *Sargassum* on a fringing reef on Viti Levu, Fiji. In the Society Islands, maximum densities of amphipods in similar habitats rarely exceeded 400 m^{-2}.

Biogeographically, the shallow-water amphipod fauna of the Society Islands can be seen to be most closely allied to that of Fiji, Tonga and New Caledonia (five uniquely shared species) and only remotely to that of Hawaii (one uniquely shared pair of sister species. Omitting the new species currently unknown outside the Society Islands, the remainder are broadly central west Pacific or Indo-Pacific, one (*Hyale affinis)* is eastern Polynesian (Niue, Society Islands, Gambier, Hawaii) and one (*Bemlos dentischium*) is Atlanto-west Pacific (Florida, Bahamas, Tonga, Western Samoa, Society Islands).

Figures and descriptions of five species and one subspecies new to science are provided, along with figures and comments on five species which either show variation

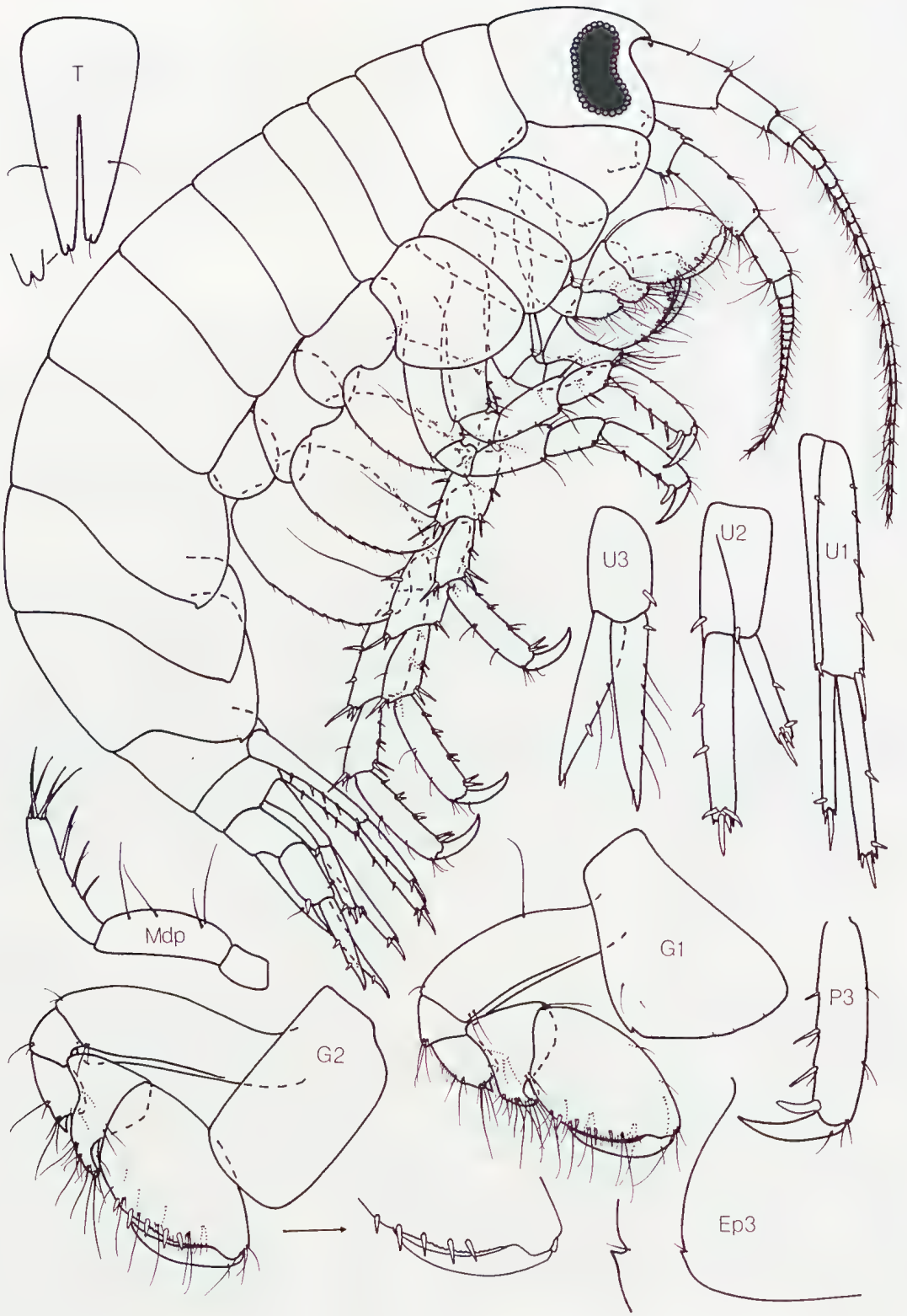

Fig.1. *Ronco sosa* Barnard, male, 2.5 mm, Bora Bora.

from previously described material, are new to the South Pacific or have not been fully figured before. Species previously figured and described from Fiji (Myers, 1985c), Niue (Myers, 1986a) or Tonga (Myers, 1986b) and which show no significant differences are simply recorded in Table 1. All material is deposited in the collections of the Australian Museum, Sydney.

Abbreviations used in figures. A1-A2 = Antenna 1-2; C3-4 = Coxa 3-4; Ep1-3 = Epimera 1-3; G1-G2 = Gnathopods 1-2; Hd = Head; J = Juvenile; L = Labium; Mdp = Mandible palp; Mx1 = Maxilla 1 inner plate ; p3-7 = Pereopods 3-7; PER = Pereon; T = Telson; U1-3 = Uropods 1-3.

Eusiridae

Ronco sosa Barnard

Fig. 1

Ronco sosa Barnard, 1965: 494, fig. 8.

Remarks. Present material agrees well with the description by Barnard (1985) of material from Micronesia. It appears to differ only in the more indented telsonic apices.

Tethygeneia pacifica (Schellenberg)

Fig. 2

Pontogeneia pacifica Schellenberg, 1938: 35, fig. 17. -Barnard, 1955: 5. -Barnard, 1970: 110, fig. 62-64. -Ledoyer, 196: 127,fig. 6.
Tethygeneia pacifica. -Barnard, 1972: 198. -Ledoyer, 1982: 415,fig. 157. -Ledoyer, 1984: 59, fig. 28.

Remarks. This species appears to have a wide Indo-Pacific distribution, but has been recorded from few, widely separated localities. The only previous record of the species from the South Pacific is that of Ledoyer (1984) from New Caledonia.

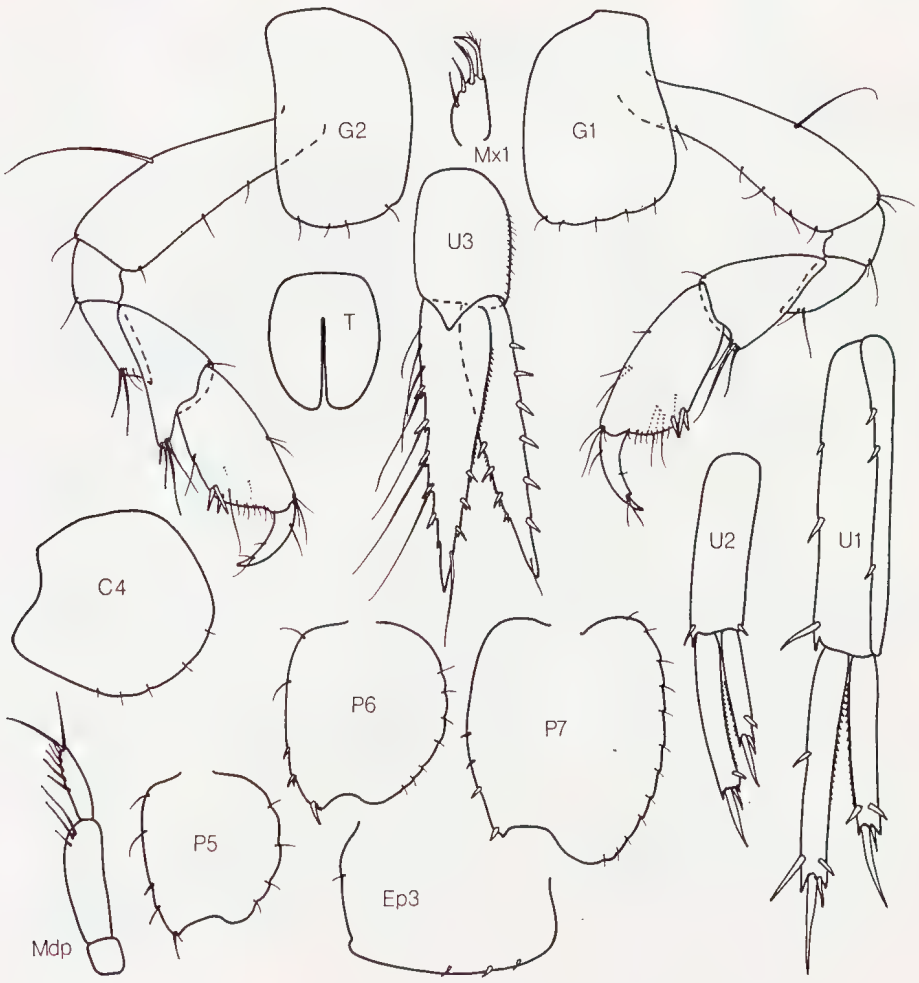

Fig.2. *Tethygeneia pacifica* (Schellenberg), male, 5.0 mm,Tahiti.

Table 1. Annotated list of species recorded from the Society Island.

Species	Stn	Male	Female	Juv	Distrib.
EUSIRIDAE					
Ronce sosa Barnard, 1965	11	1	-	1	F
Tethygeneia pacifica (Schellenberg, 1938)	1	1	-	-	F
AMPHILOCHIDAE					
Amphilochus menehune Barnard, 1970	6	-	3	-	C
	10	-	1	-	
	11	3	5	3	
	22	4	4	2	
Gitanopsis tai Myers, 1985c	23	1	-	-	C
	24	16	7	7	
	25	1	-	-	
ANAMIXIDAE					
"Leucothoides"	7	-	1	-	F
	23	-	1	-	
	24	1	-	-	
HYALIDAE					
Hyale affinis Chevreux, 1907	1	12	30	24	D
	2	19	17	6	
Hyale galateae distorta Myers, 1985c	22	65	29	2	CE
TALITRIDAE					
Platorchestia platensis (Kroyer, 1845)	12	2	8	3	C
PHLIANTIDAE					
Pereionotus alaniphlias Barnard, 1970	23	1	2	-	C
	24	-	2	-	
	26	-	1	-	
LYSIANASSIDAE					
Parambasia nui Myers, 1985c	20	1	-	-	C
MELITIDAE					
Elasmopus integer n.sp.	10	4	3	-	F
Elasmopus seticarpus Myers, 1985c	7	3	13	-	C
	25	1	1	-	
Maera lindsae n.sp.	7	-	6	2	F
Maera mooreana n.sp.	24	-	-	1	F
	25	2	2	-	
	27	-	1	-	
Maera octodens Sivaprakasam, 1968	23	1	1	-	C
Maera pacifica Schellenberg, 1938	10	-	1	-	C
	11	-	1	-	
Maera serrata Schellenberg, 1938	6	1	-	-	C
	14	-	1	-	
	19	-	1	-	
	25	3	7	-	
Parelasmopus suensis (Haswell, 1880)	6	1	1	-	C
	7	8	13	2	
	15	2	2	5	
	23	4	6	6	
	24	4	9	9	
	25	4	11	2	
	26	3	1	-	
AMPITHOIDAE					
Ampithoe ramondi (Audouin, 1826)	2	1	3	-	CD
	4	-	3	-	
	6	6	13	-	
	7	3	12	-	
	8	3	11	-	
	11	5	9	-	
	13	1	1	-	
	16	2	8	-	
	17	3	5	-	
	18	17	23	-	
	19	3	7	-	
	20	9	13	-	
	21	2	9	-	
	22	-	1	-	
	23	-	3	2	
	24	4	8	-	
	26	8	22	-	
	27	3	6	-	
Cymadusa brevidactyla (Chevreux, 1907)	3	1	6	-	CE
	10	3	10	8	
Cymadusa pilipes (Ledoyer, 1984)	2	-	1	-	CE
	15	2	1	-	
	19	-	2	-	
	20	2	3	-	
	24	2	2	4	
Paragrubia vorax Chevreux, 1901	1	-	1	-	CE
	17	-	1	-	
	18	1	7	-	
	20	1	6	-	
	22	-	1	-	
Pleonexes auriculata Rabindranath, 1972	1	13	37	-	F
	2	6	18	-	
	3	3	6	-	
	4	1	2	-	
	11	28	66	-	
	17	7	14	-	
	18	20	48	-	
	19	1	-	-	
	20	3	8	-	
	21	1	3	-	
	22	6	21	-	
	24	1	-	-	
	26	1	-	-	
Pleonexes kulafi Barnard, 1965	5	4	5	-	CE
	6	10	24	-	
	7	2	6	-	
	8	21	43	-	
	9	3	6	-	
	10	2	7	-	
	11	3	2	-	
	16	4	3	-	
	26	2	3	-	
	27	31	66	-	
ISAEIDAE					
Cheiriphotis rotui n.sp.	16	-	1	-	F
	26	-	1	-	
	27	1	4	1	
Chevalia aviculae Walker, 1904	23	1	1	-	C
	24	2	2	3	
Gammaropsis digitata (Schellenberg, 1938)	1	-	3	1	C
	4	-	-	1	
Gammaropsis setifera (Schellenberg, 1938)	17	-	1	-	C
	18	1	1	2	
	20	-	1	-	
ISCHYROCERIDAE					
Jassa socia n.sp.	6	5	4	-	F
	7	1	1	-	
	8	2	1	-	
	9	16	26	3	
	11	16	17	2	
	17	-	1	-	
	20	-	2	-	
	21	-	1	-	
	24	1	3	-	
	26	-	1	-	
AORIDAE					
Bemlos dentischium taparum (Myers, 1985b)	4	-	1	-	BE
	6	4	5	-	
	7	8	12	3	
	13	1	1	-	
	18	1	-	-	
	23	1	2	-	
	24	-	2	-	
Globosolembos ovatus Myers, 1985a	23	4	5	-	AC
	24	1	1	-	
	25	2	-	-	
	26	8	6	-	
	27	-	1	-	
COROPHIIDAE					
Polynesoecetes kekeae n.sp.	26	1	-	-	F

See A: Myers, 1985a, B: Myers, 1985b, C: Myers, 1985c, D: Myers, 1986a, E: Myers, 1986b, F: Present paper

Anamixidae

"Leucothoides "

Fig. 3

Remarks. Three specimens of a *"Leucothoides "* were collected at Huahine and Moorea, but were not accompanied by hyperadult male *Anamixis* or *Paranamixis*. In general they most closely resemble the presumed *"Leucothoides"* - form of *Paranamixis madagascarensis* Ledoyer (see Myers, 1985c) but the basis of pereopod 7 is unscalloped, and the larger of the two basally immersed spines on the distal end of the carpal prologation is somewhat more strongly serrated.

Phliantidae

Pereonotus alaniphlias (Barnard)

Fig. 4

Palinotus alaniphlias Barnard, 1970: 227, fig. 148-150.
Pereonotus alaniphlias. -Ledoyer, 1978: 309. -Ledoyer, 1979 : 122,fig.78. -Myers, 1985c: 130, fig. 103. -Ledoyer, 1986: 869, fig. 342.

Remarks. The male of this species is recorded for the first time from the Pacific. It differs from the female in the structure of pereonite 1, pereopod 7 and uropods 1-2. The anterior lobe of pereonite 1 is truncated and overhangs the

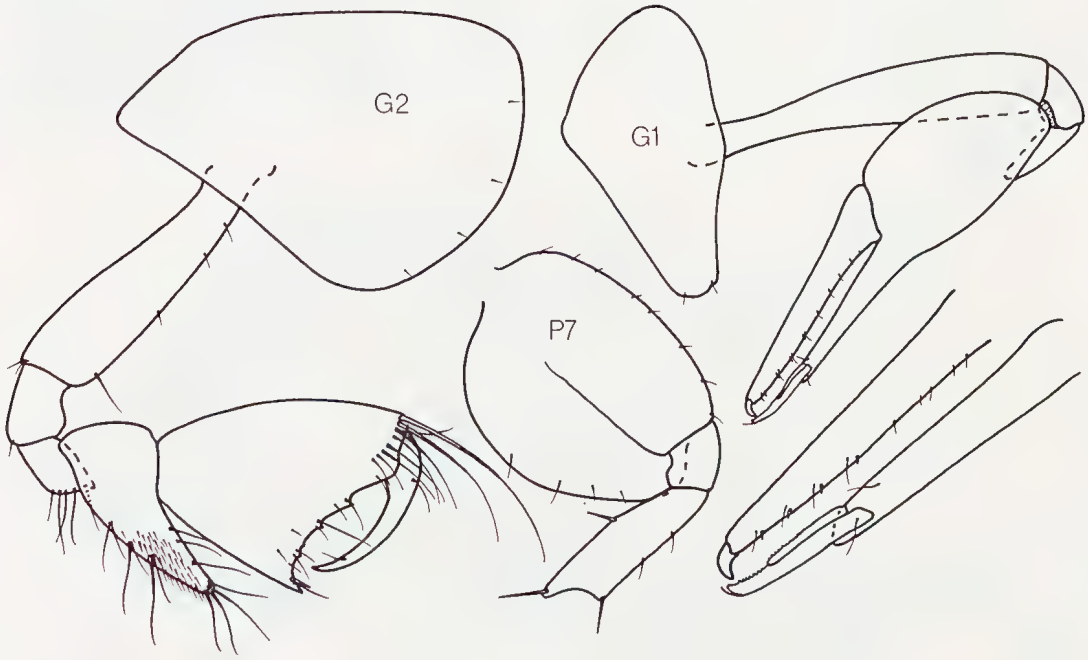

Fig.3. *"Leucothoides "* female, 2.0 mm, Huahine.

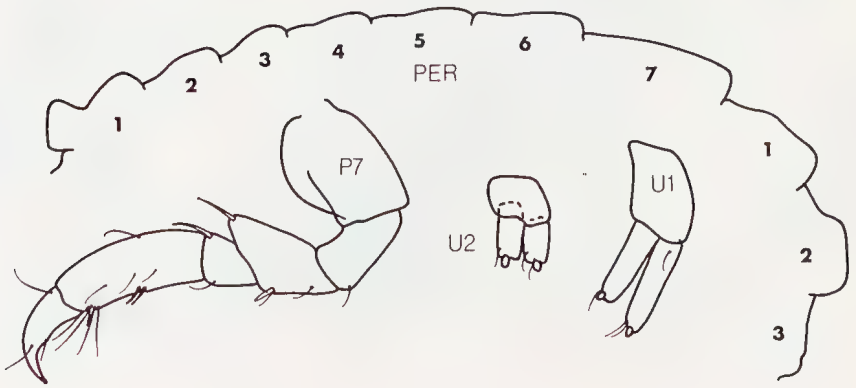

Fig.4. *Pereionotus alaniphlias* (Barnard), male, 3.5 mm, Moorea.

head, pereopod 7 basis has an evenly convex posterior margin, uropod 1 bears shorter rami than the female, and uropod 2 is biramous, with short, stout rami. The male of this species has recently been figured from Madagascar by Ledoyer (1986), but in that material, pereonite 1 has an evenly rounded anterior lobe, and the basis of pereopod 7 is ovatoquadrate in the male, and has a rounded posterior margin in the female, i.e. the reverse of the situation shown here.

Melitidae

Elasmopus integer n.sp.

Figs 5--6

Type material. HOLOTYPE male 4.8 mm. AM P38607, Bora Bora, 1 km north of Paoaoa, among *Padina* in sheltered lagoon, 29 Nov 1986. PARATYPES (6) AM P38608 same data as above.

Description. Length 4.8 mm. Head with subocular notch. Eye large, subround. Mandible palp article 3 strongly falcate. Antenna 1 and 2 moderately setose. Antenna 2 about half body length, flagellum with about 17 articles; accessory flagellum with 2 articles, the terminal article rudimentary. Antenna 2 slender, about two thirds antenna 1. Gnathopod 1 coxa anterodistal corner scarcely produced; carpus and propodus subequal. Male gnathopod 2 coxa deeper than broad; basis stout, anterodistal margin with about 6 strong spines; carpus short, cup shaped; propodus over 3 times length of carpus, palm oblique, with 2 submarginal distal humps separated from a submarginal, triangular proximal tooth; dactylus falcate, shorter than palm. Female gnathopod 2 basis more slender; carpus subtriangular; propodus twice length of carpus, palm very oblique without teeth. Pereopods 5-7 basis posterior margin weakly crenulate, with long setae situated in some of the depressions; all articles with long setae on the

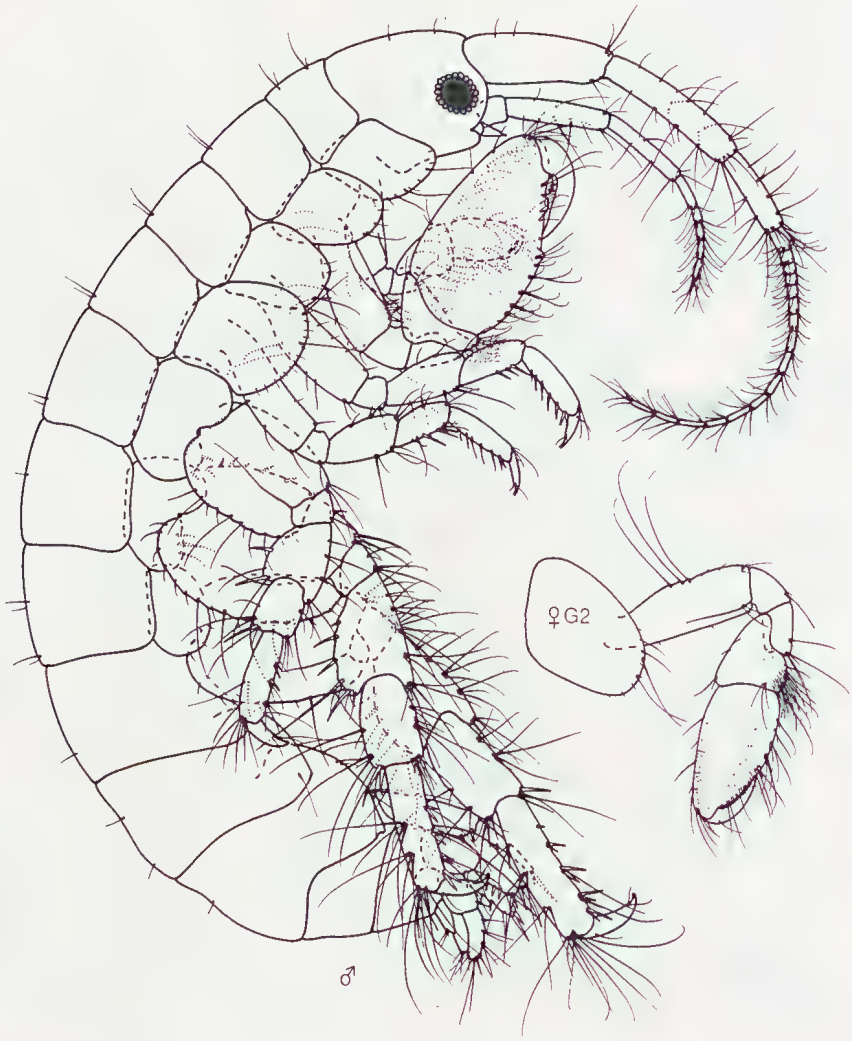

Fig.5. *Elasmopus integer* n.sp. male, Paratype 4.8 mm, Bora Bora, female, 4.6 mm, Bora Bora.

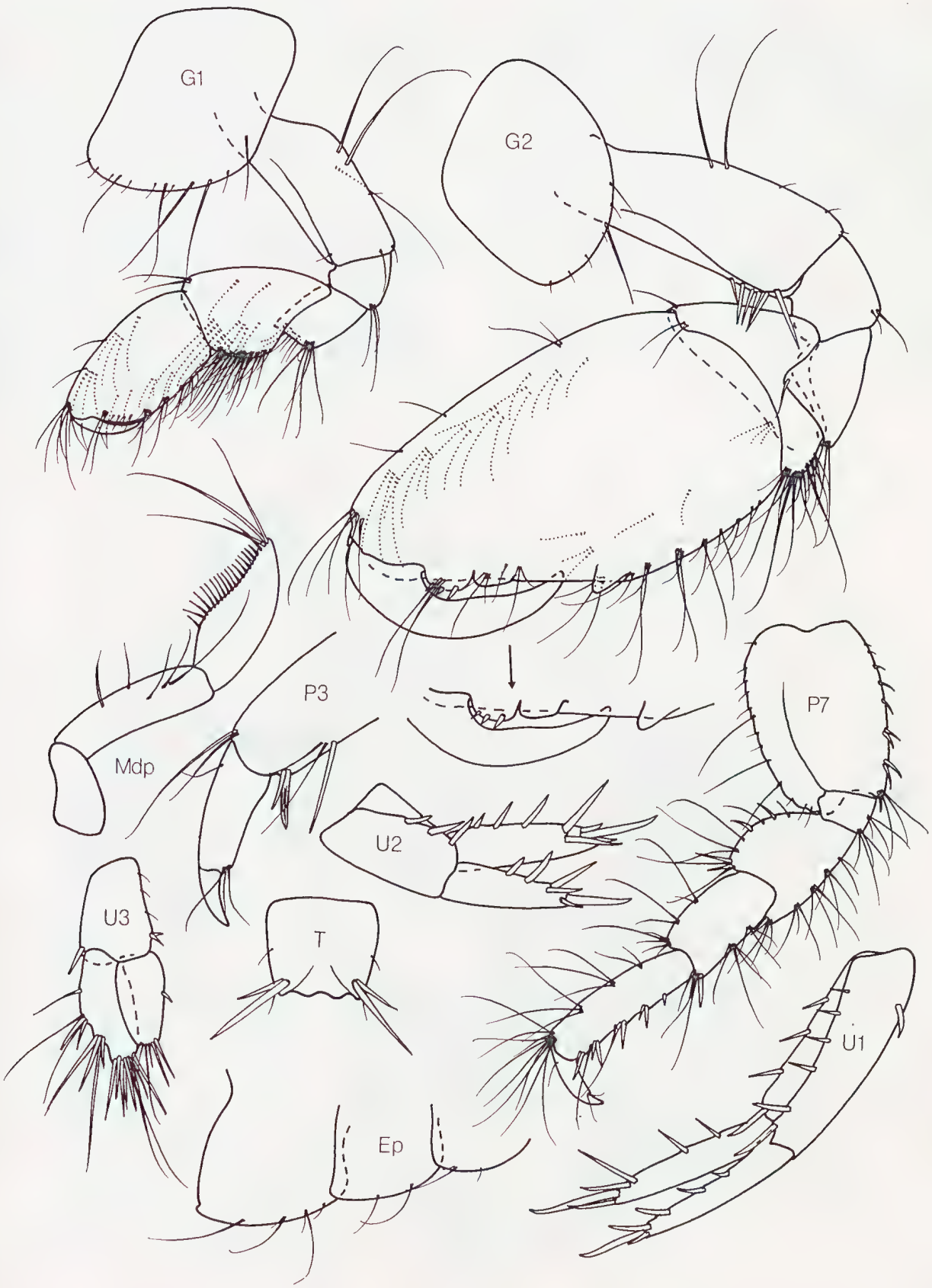

Fig.6. *Elasmopus integer* n.sp. male, Paratype 4.8 mm, Bora Bora.

anterior and posterior margins. Epimera with long setae on lower margins. Epimeron 3 posterodistal corner with small tooth. Uropod 1 slender. Uropod 2 stout, spinous. Uropod 3 outer ramus subequal with peduncle, slightly longer than inner ramus and with long spines and spine setae. Telson subsquare, entire, but with dorsodistal depression, apices each with a pair of unequal spines.

Remarks. This species is very close to *E. hooheno* Barnard, from which it differs in the form of the male gnathopod 2 palm, in the non-spatulate locking spine of pereopods 3-4, unnotched posterior margin of epimeron 3 and entire telson, more strongly setose pereopods 5-7, longer inner ramus of uropod 3 and more elongate spines on uropod 3. An entire telson is known in only one other species of *Elasmopus* viz. *E. takamotus* Myers from Niue Island.

Distribution. Currently known only from the type locality.

Etymology. From the latin *integer* = entire, referring to the entire telson.

Maera lindsae n.sp.

Figs 7-8

Type material. HOLOTYPE 4.0 mm AM P38623, Huahine, Lagon de Fare, among *Halimeda* from lagoon, 27 Nov 1986. PARATYPES (7) AM P38623 same date as above.

Description. Length 4.0 mm. Head with subocular notch. Eye small, subround. Mandible palp rod-shaped, article 3 the longest, with 4 terminal setae and 1

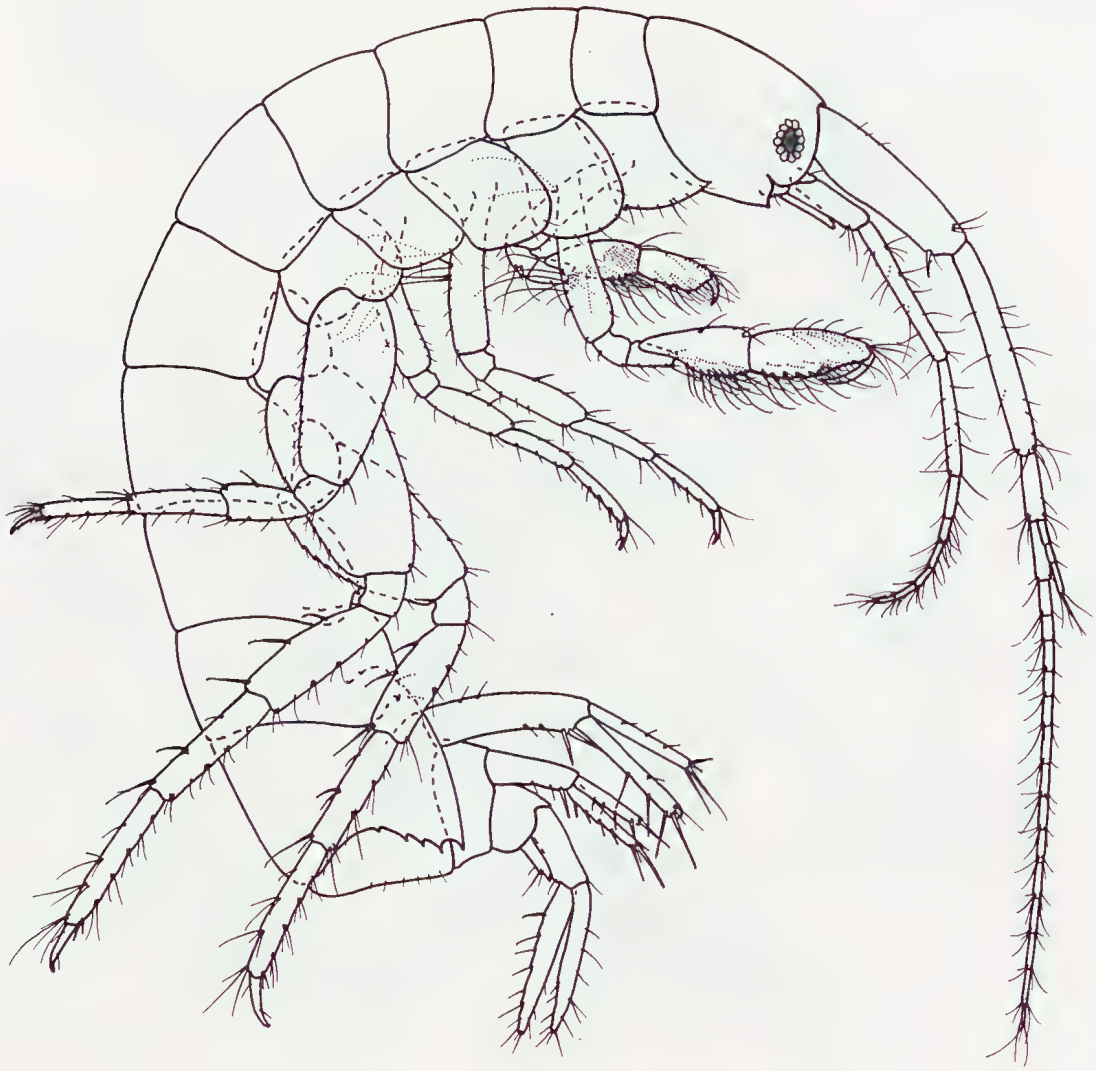

Fig.7. *Maera lindsae* n.sp. female, Paratype 4.0 mm, Huahine.

medioposterior seta. Antenna 1 elongate, slender, two thirds body length, flagellum with about 15 articles; acessory flagellum with 4 articles, the terminal article rudimentary. Antenna 1 slender, about two thirds antenna 1. Gnathopod 1 coxa anterodistal corner strongly produced, very acute, posterodistal corner with small tooth; carpus and propodus slender, carpus distinctly the longer. Female gnathopod 2 coxa deeper than broad; merus with small, acute posterodistal tooth; carpus and propodus slender, propodus the longer with very oblique unornamented palm; dactylus fitting palm. Epimera 1-2 with small posterodistal tooth. Epimeron3 posterior margin scalloped, with 5 acute teeth. Uropods 1-2 slender. Uropod 3 rami elongate, subequal, over one and a half times length of peduncle, with slender marginal spines, peduncle with strong spines. Telson deeply divided, lobes divergent, acute, with mediodistal tooth on inner margin bearing a stout spine at its base. Male unknown.

Remarks. This species shows affinity with *Maera hamigera* Haswell, but differs from that species in its more elongate antenna 1, smaller eye, more strongly scalloped epimeron 3, single toothed epimera 1-2, and more widely separated and unequal telsonic teeth. It also shows some similarity to *Maera* sp. A of Barnard (1970) but differs from that species in the strongly acute coxa 1, unexcavate palm of gnathopod 2 and in having mandible palp article 3 longer than article 2.

Distribution. Currently known only from the type locality.

Etymology. Named after my daughter Lindsay in appreciation for her help in the field.

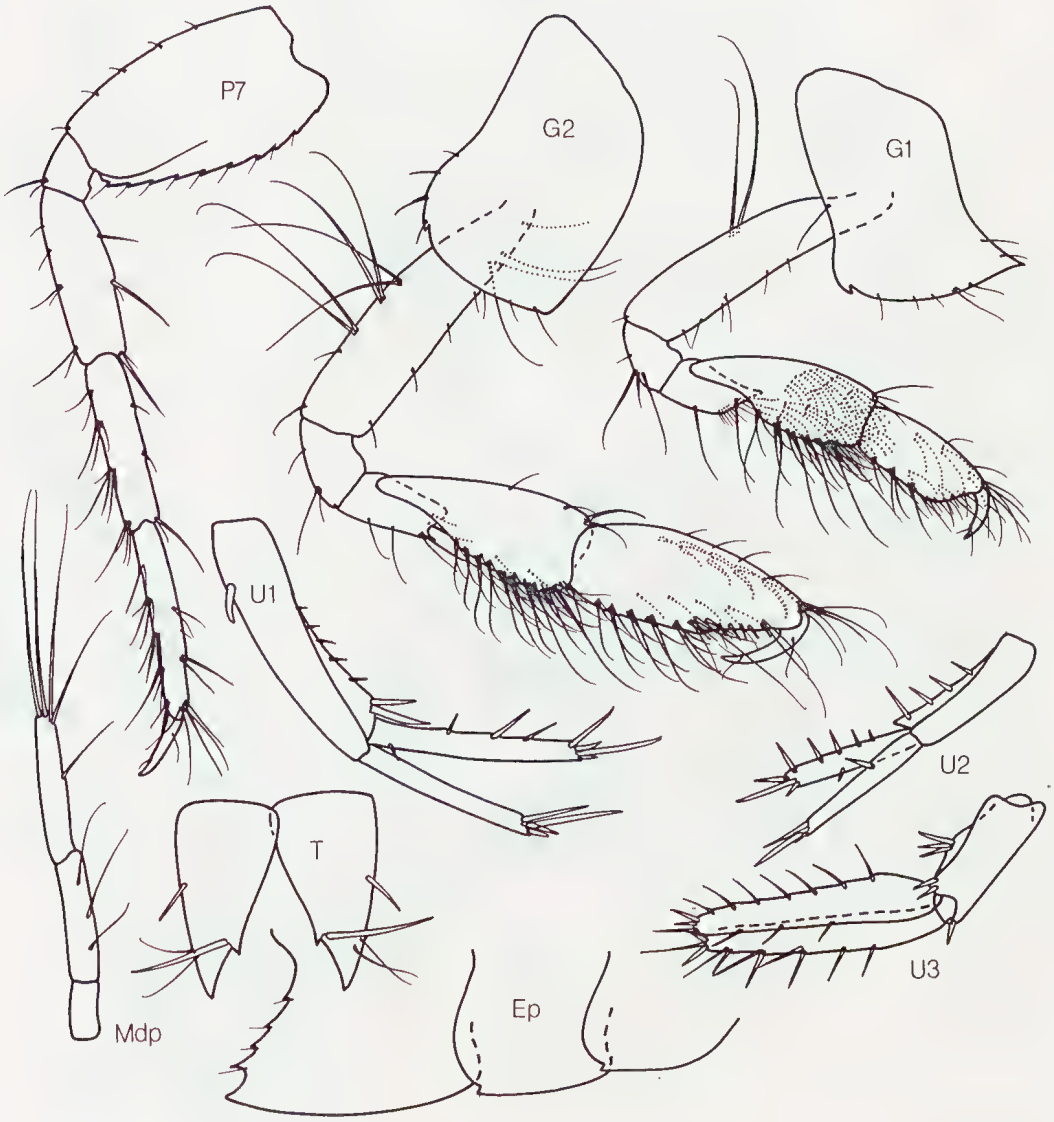

Fig.8. *Maera lindsae* n.sp. female, Paratype 4.0 mm, Huahine.

Maera mooreana n.sp.

Figs 9-10

Type material. HOLOTYPE male 3.0mm AM P38625, Moorea, north-east entrance to Cook's Bay, coral rock and *Porolithon* from lagoon, 11 Dec 1986. PARATYPES (3) AMP38626 same data as above. Other material. 1 female AM P38627 Moorea, north-east entrance to Cook's Bay, *Padina* from jetty, 11 Dec 1986; 1 immature, AM P38628, same locality and date, in *Pocillopora* from lagoon.

Description. Length 3.0 mm. Head without subocular notch. Eye large, subround. Mandible palp article 3 approximately parallel sided, slightly shorter than article 2, with 3 terminal setae and 1 medioposterior seta. Antenna 1

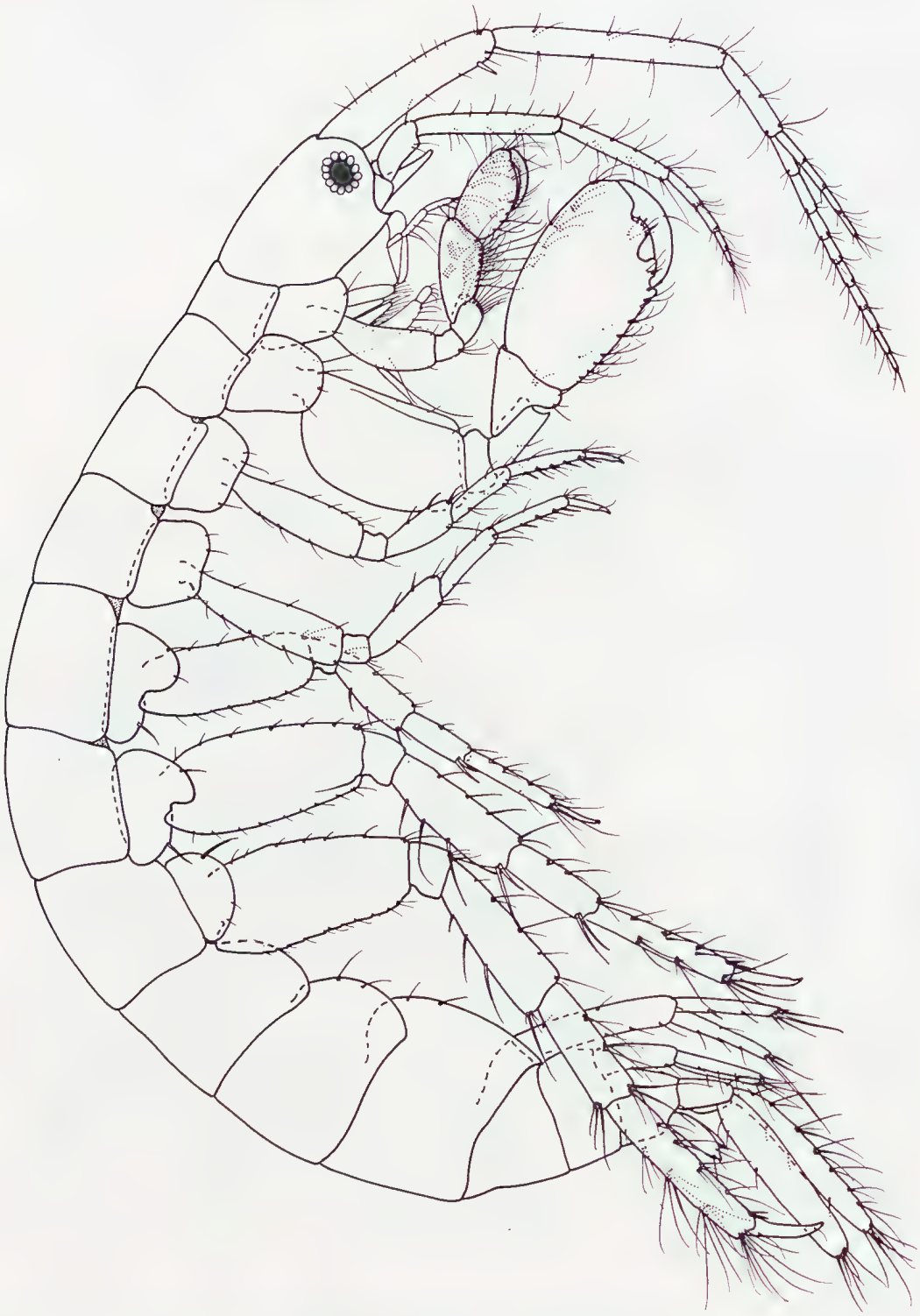

Fig.9. *Maera mooreana* n.sp. male, Holotype 3.0 mm, Moorea.

Fig.10. *Maera mooreana* n.sp. male, Holotype 3.0 mm, Moorea, female, 3.0 mm, Moorea.

short, less than half body length; peduncular articles 1 and 2 elongate; flagellum shorter than combined length of peduncular articles 2+3, with up to 10 articles; accessory flagellum elongate with 5 articles, the terminal article rudimentary. Antenna 2 slender, about two thirds length of antenna 1, with up to 5 articles. Gnathopod 1 coxa subsquare, slightly produced anterodistally, obtuse; carpus and propodus subequal. Male gnathopod 2 coxa as broad as deep; basis robust, less than twice as long as broad; merus with acute tooth at posterodistal corner; carpus short subtriangular; propodus almost three times length of carpus, palm spinous, with broad round-bottom excavation and small defining tooth; dactylus fitting palm. Female gnathopod 2 basis slender, almost 3 times as long as broad; carpus and propodus similar to that of male, but palm lacking excavation or tooth. Pereopods 3-4 slender.Pereopods 5-7 basis posterior margin very weakly toothed. Epimera 1-2 rounded. Epimeron 3 posterior margin smooth, with acute posterodistal tooth. Uropods 1-2 slender. Uropod 3 rami greatly elongated, almost 3 times length of peduncle, outer ramus setose. Telson deeply divided, lobes weakly divergent, distally bifid, each lobe bearing strong, subequal spines.

Remarks. This species shows some similarities with *Maera inaequipes* (Costa), in its unnotched head, and broadly similar male gnathopod 2. It differs from that species however, in its non acute coxa 1, weakly setiferous mandible palp article 3, totally different uropod 3 and unexpanded posterodistal margin of pereopods 5-7, as well as in the untoothed palm of the female gnathopod 2.

Distribution. So far recorded only from Moorea.

Etymology. Named after the type locality.

Ampithoidae

Pleonexes auriculata Rabindranath

Figs 11-12

Ampithoe (Pleonexes) auriculata Rabindranath, 1972: 171, fig. 7.

Remarks. Present material agrees well with the description of Rabindranath (1972) from the coast of India and represents the first record from the Pacific.

Isaeidae

Cheiriphotis rotui n.sp.

Figs 13-14

Type material. HOLOTYPE male 2.0 mm AM P38629, Moorea, north-east entrance to Cook's Bay, *Padina* from jetty, 11 Dec 1986. PARATYPES (5) AM P38630 same data as above.Other material. 1 female AM P38631, Moorea, north-east entrance to Cook's Bay, *Padina* on bed of sea urchin spines, 2 Dec 1986. 1 female AM P38632, Moorea, north-east entrance to Cook's Bay, *Padina*-covered rocks from lagoon, 13 Dec 1986.

Description. Length 2.6 mm. Head lateroventral margins moderately recessed in female, very recessed in male for accommodation of enlarged antenna 2 peduncle. Mandible palp article 2 the longest; article 3 clavate with very long distal setae. Antenna 1 a little less than two thirds body length, primary flagellum a little longer than peduncle with up to 12 articles; accessory flagellum with 4 articles, the terminal article rudimentary. Male antenna 2 peduncular article 2 massive; articles 3 and 4 enlarged, each with posterodistal tooth; article 5 subequal in length with article 4 but a little more slender; flagellum with 5 articles, article 1 enlarged. Female antenna 2 slender; flagellum with 6 articles. Coxa 1 the largest, produced forward, distally setiferous. Gnathopod 1 basis, carpus and propodus slender; carpus a little longer than propodus, palm oblique defined by a spine; dactylus elongate and slender. Male gnathopod 2 basis stout; carpus short, cup shaped; propodus enlarged, anterior and posterior margins approximately parallel, palm with 2 teeth, separated by a flat-bottomed excavation, the proximal tooth the larger; dactylus overlapping proximal tooth. Female gnathopod 2 coxa deep; basis moderately stout; propodus more than 3 times length of cup-shaped carpus, palm sinuous defined by a spine. Pereopods 3-4 basis broad. Pereopods 5-7 basis, ischium and merus setose. Epimera 1-2 with a small posterodistal tooth. Epimeron 3 rounded. Uropod 1 elongate. Uropod 2 short, peduncle subsquare, rami subequal, shorter than peduncle. Uropod 3 peduncle expanded, broader than long, outer ramus short, a little shorter than peduncle,inner ramus rudimentary with a single distal spine. Telson broader than long.

Remarks. Present material most closely resembles *Cheiriphotis durbanensis* K.H. Barnard, but differs from that species and indeed all known species of the genus by the secondary sexual enlargement of the peduncular articles of antenna 2 in the male.

Distribution. So far known only from Moorea.

Etymology. Named after Mount Rotui which overlooks Cook and Opunohu Bays, Moorea.

Ischyroceridae

Jassa socia n.sp.

Fig. 15

Type material. HOLOTYPE male 1.8 mm AM P38633, Bora Bora, 1 km north of Paoaoa, in *Turbinaria ornata* from a sheltered lagoon, 29 Nov 1986. PARATYPES (44) AM P38634, same data as above. Other material. 1 male, 3 females, AMP38635, Moorea, north-east entrance

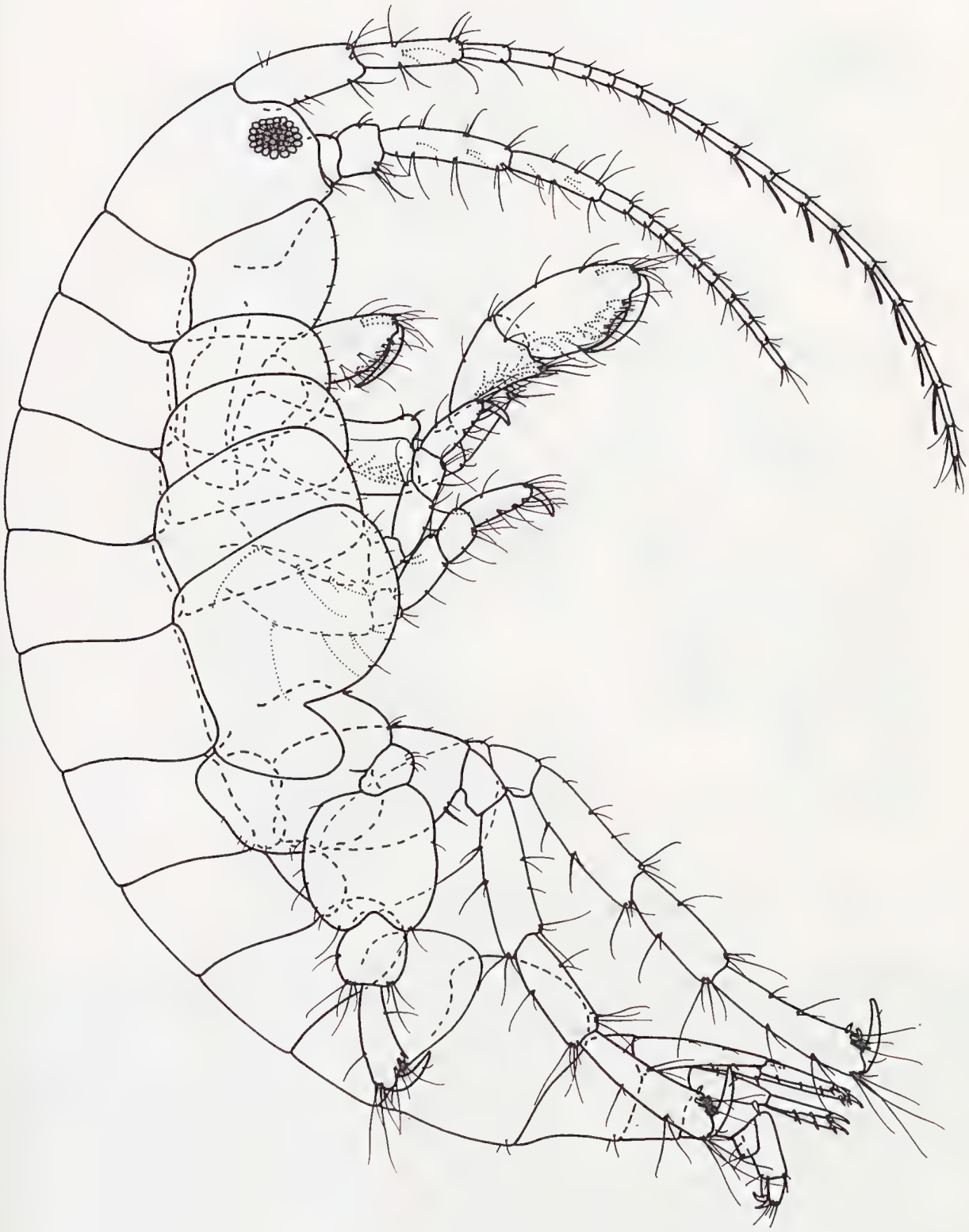

Fig.11. *Pleonexes auriculata* Rabindranath, male, 5.0 mm, Moorea.

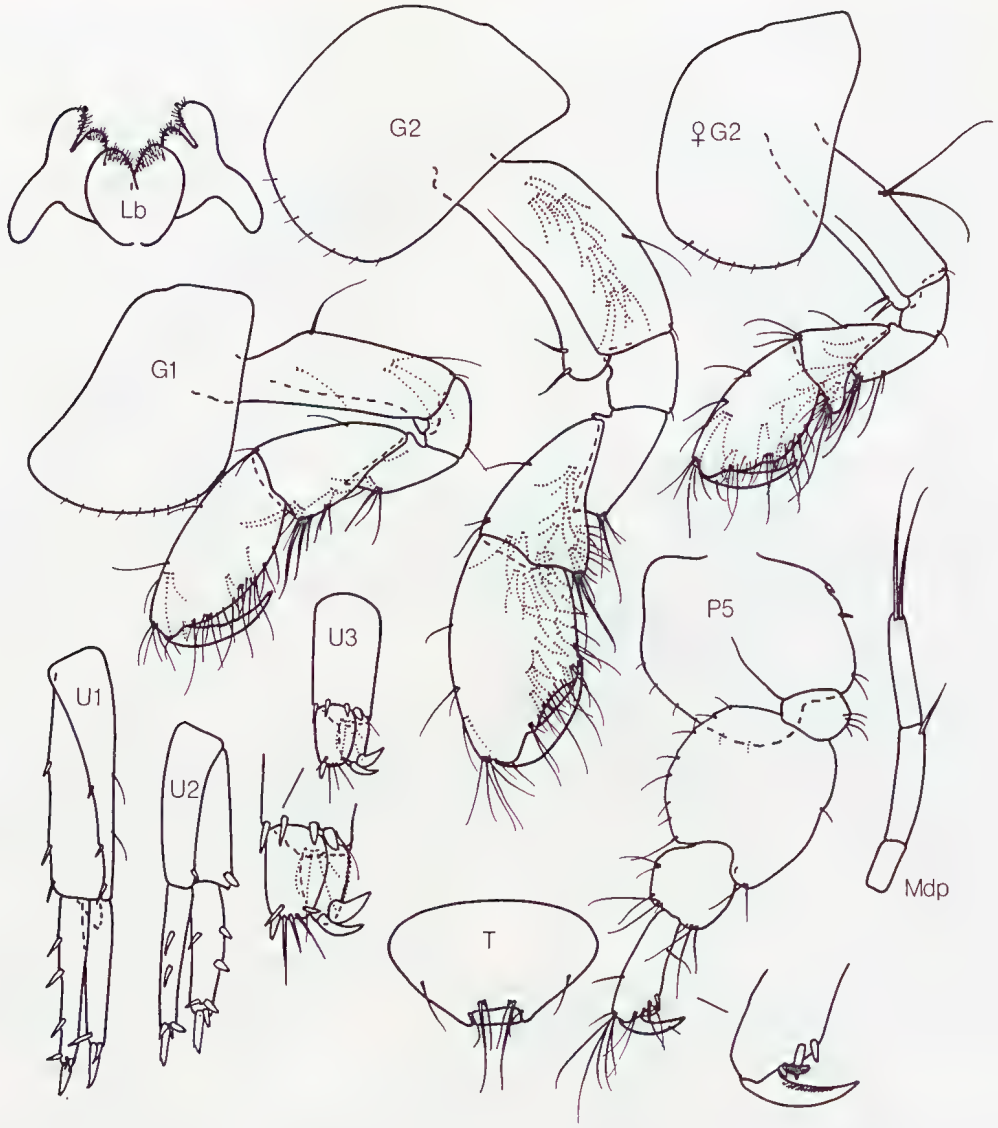

Fig.12. *Pleonexes auriculata* Rabindranath, male, 5.0 mm, female, 5.4 mm, Moorea.

to Cook's Bay, *Pocillopora,* 11 Dec 1986; 1 male, 1 female, AM P38636, Huahine, Lagon de Fare, *Halimeda* from lagoon, 27 Nov 1986; 5 males, 4 females, AM P38637, Huahine, Lagon de Fare, *Turbinaria ornata* from lagoon, 27 Nov 1986; 30, AM P38638, Bora Bora, Viatape, *Sargassum* from lagoon, 29 Nov 1986; 1 female, AM P38639, Moorea, north-east entrance to Cook's Bay, *Padina*-covered rocks from lagoon, 11 Nov 1986; 2 males, 1 female, AM P38640, Huahine, Lagon de Fare, *Padina*-covered rocks from lagoon, 27 Nov 1986; 1 female, AM P38641, Moorea, near Ilot Tiahura, *Dictyota* in lagoon, 4 Dec 1986; 2 females, AM P38642, Moorea, near Ilot Tiahura, *Turbinaria ornata* with epiphytes from lagoon, 4 Dec 1986; 1 female, AM P38643, Moorea, near Ilot Tiahura, *Sargassum* on inner side of barrier reef, 4 Dec 1986.

Description. Length 1.8 mm. Lateral cephalic lobes mammiliform. Antenna 1 article 1 short, article 2 and 3 subequal, primary flagellum shorter than combined length of peduncular articles 2 and 3, accessory flagellum with 1 long and 1 rudimentary article. Antenna 2 a little longer than antenna 1. Mandible palp article 1 with anterodistal rounded lobe, article 3 strongly clavate. Gnathopod 1 in both sexes and gnathopod 2 of female similar, propodus larger than carpus, subovoid. Male gnathopod 2 basis with flange on anterior margin, merus blunt, carpus small, cup shaped, propodus becoming elongate with maturity, posterior margin with stout, thumb-like proximal process and smaller distal process, dactylus elongate and falciform, opposable to proximal process of propodus. Pereopods 3-7 propodus with weakly developed locking spines. Uropod 3 outer ramus with 6 scarcely reverted cusps, inner ramus with a single, basally immersed spinule. Telson pointed with a stout spine on each side.

Remarks. *Jassa socia* differs from *Jassa lilipuna*

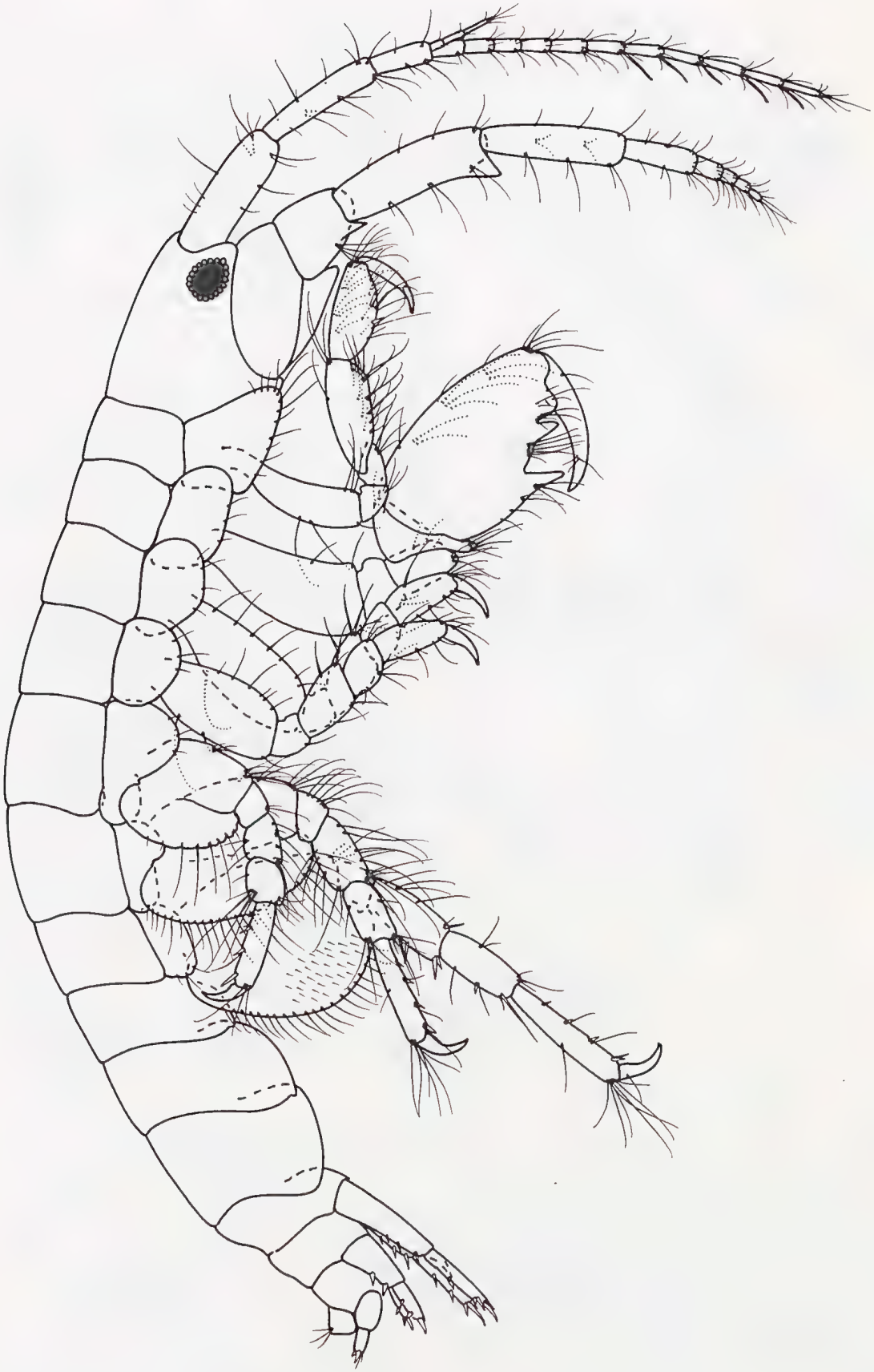

Fig.13. *Cheiriphotis rotui* n.sp. male, Holotype 2.0 mm, Moorea.

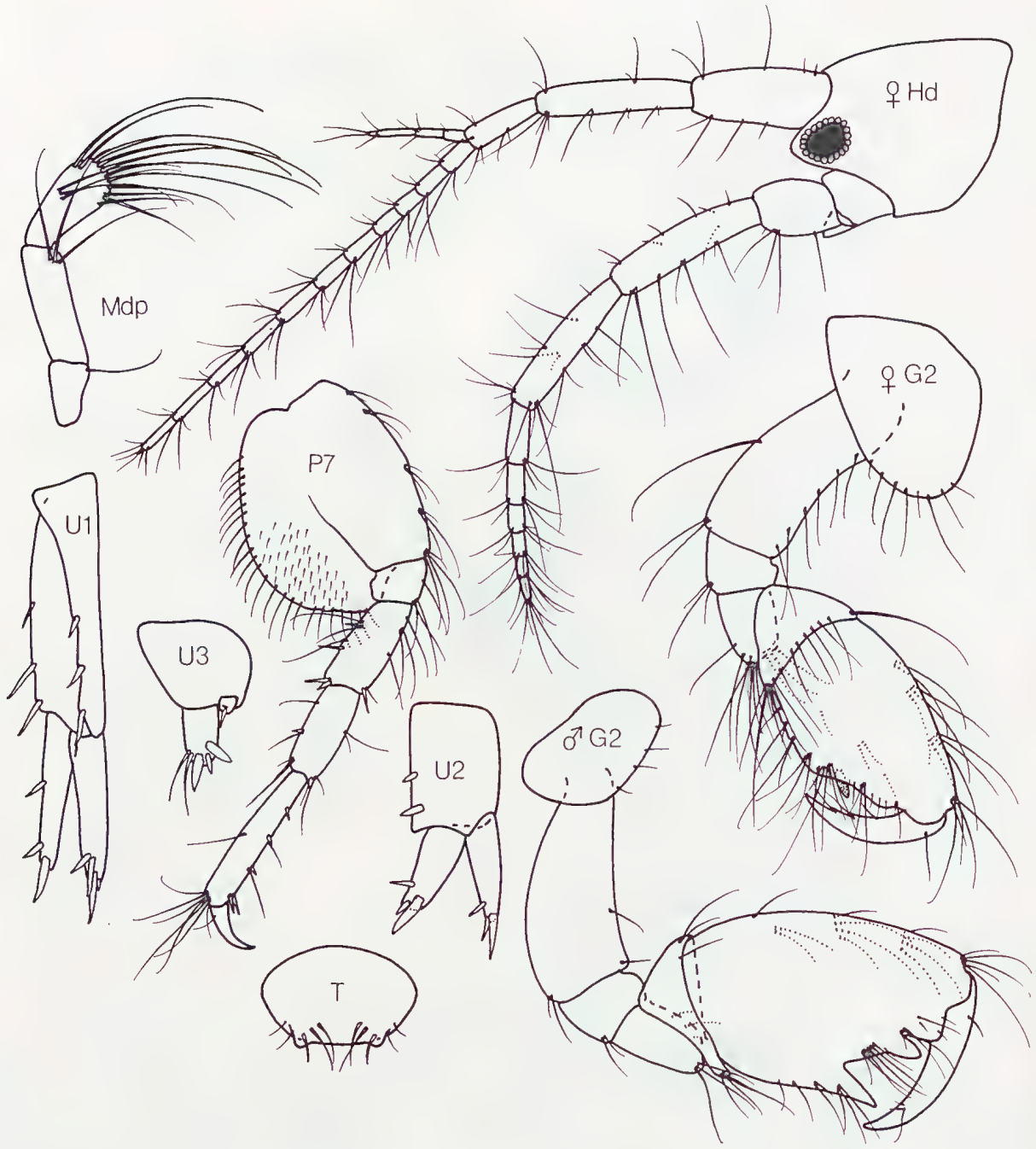

Fig.14. *Cheiriphotis rotui* n.sp. male, Holotype 2.0 mm, female, 2.0 mm, Moorea.

Barnard (1970) from Hawaii in the short article 1 of antenna 1, the stronger flange on the basis and smaller proximal process on the propodus of the male gnathopod 2, the weak locking spines on the propodus of pereopods 3-7, in the presence of 6 cusps on the outer ramus of uropod 3 and in the somewhat shorter uropod 3 peduncle. Coxa 2 is not bilobed in any of the material examined, as it is in hyperadult male *J. lilipuna*. According to Conlon (personal communication) *J. lilipuna* requires a new genus.

Distribution. Huahine, Bora Bora, Moorea.

Etymology. From the latin *socius* = allied.

Corophiidae

Polynesoecetes n.gen.

Diagnosis. Urosomite 2 free, produced ventrally into a rounded plate. Urosomite 3 and telson fused dorsally. Uropod 1 biramous, inner ramus less than one third length of outer ramus. Uropod 2 absent, uropod 3 with

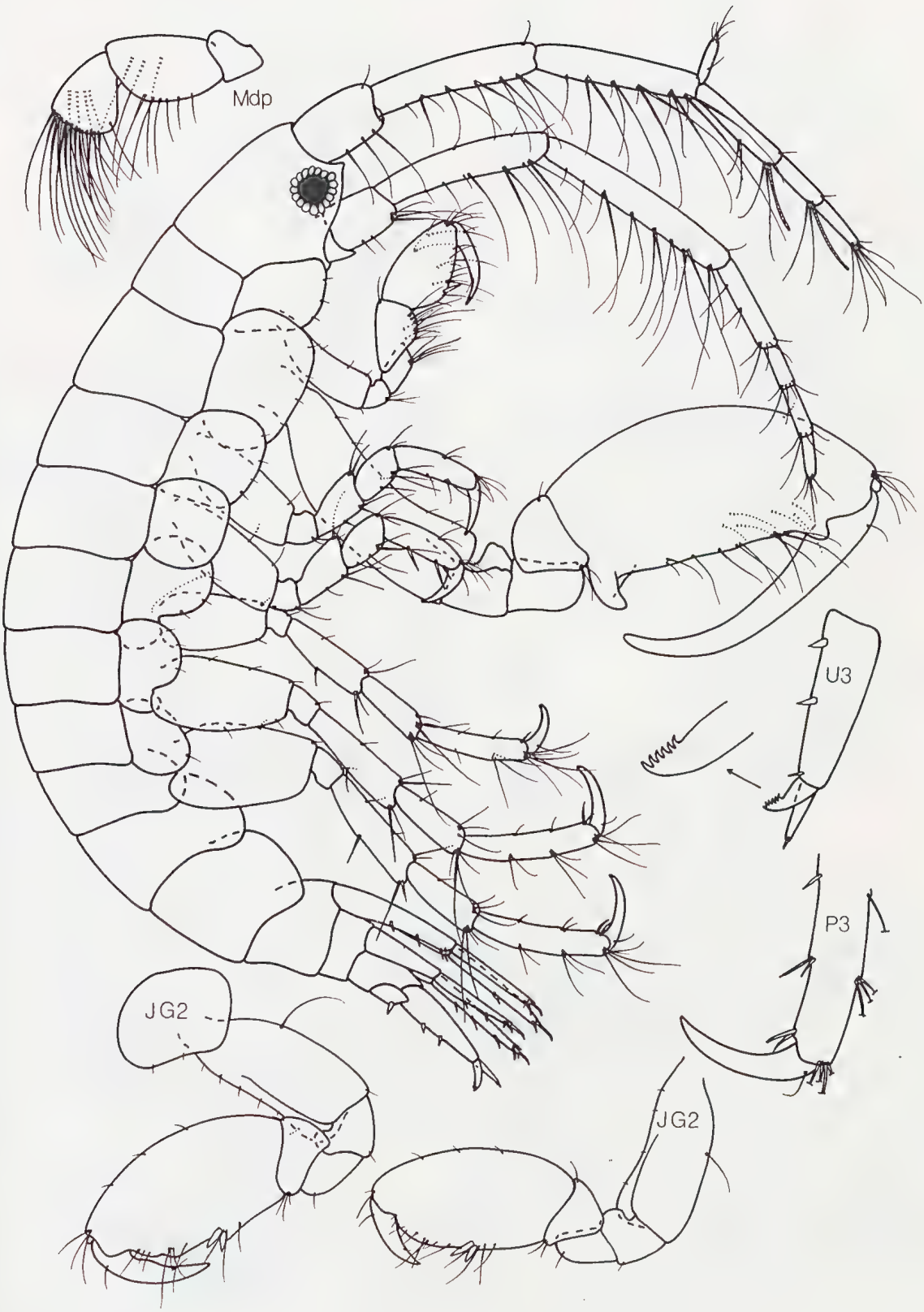

Fig.15. *Jassa socia* n.sp. male, Paratype 1.8 mm, Bora Bora.

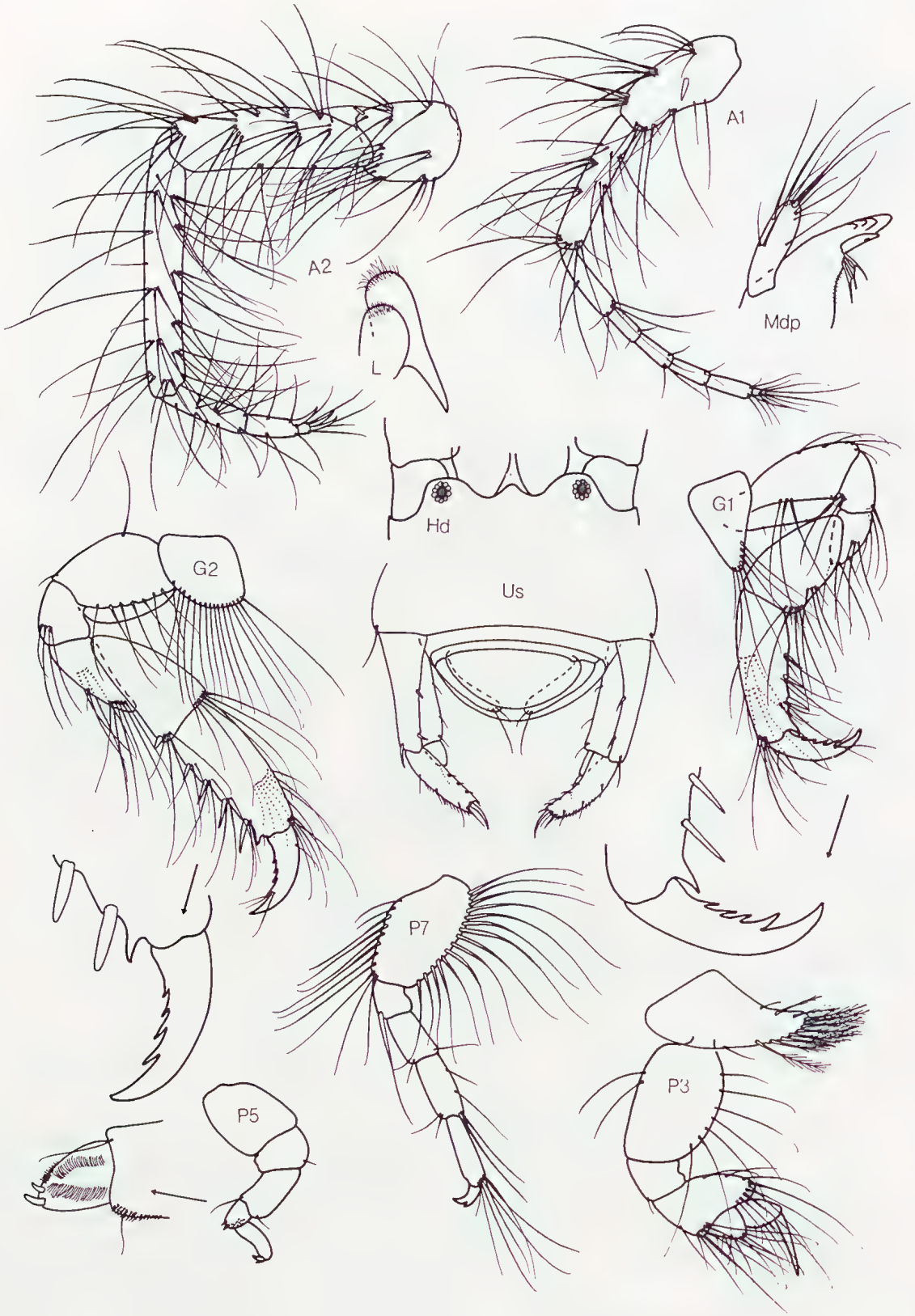

Fig.16. *Polynesoecetes kekeae* n.sp. male, Holotype, 1.8 mm, Moorea.

unexpanded peduncle, ramus absent. Rostrum rounded. Gnathopods 1-2 simple with small palmar tooth. Pereopods 5-7 dactylus with accessory tooth. Coxal plates 3 and 4 with weakly notched distal margin bearing slender plumose setae.

Polynesoecetes kekeae n.sp.

Fig. 16

Type material. HOLOTYPE male 1.8 mm AMP38645, Moorea, north-east entrance to Cook's Bay, *Padina*-covered rocks from lagoon, 11 Dec 1986.

Description. Length 1.8 mm. Head with weak rounded rostrum, eyes small. Head and cephalon lacking rows of dorsal setules. Mandible palp 1-articulate, subovoid, setiferous. Labium with mandibular projections of outer plate elongate, acute. Antennae densely setose. Antenna 1 article 1 much longer than article 3 and only a little shorter than article 2; flagellum with 6 articles, the penultimate article greatly reduced, the terminal article rudimentary. Antenna 2 stout, equal in length to head and pereon combined, article 5 longer than article 4, flagellum shorter than article 5 with 3 articles, the first article the longest, the third article reduced. Gnathopod 1 coxa triangular, distally setose; propodus longer than carpus, almost simple, but made subchelate by a strong, acute, posterodistal tooth, posterior margin with 3 strong equidistant spines; dactylus stout, posterior margin with 4 strong teeth. Gnathopod 2 similar to gnathopod 1 but larger, coxa broadly rounded and distally setose; carpus with small spine at posterodistal angle; propodus with acute posterodistal tooth and 4 equidistant spines on posterior margin. Pereopods 3-4 coxa with distal margin weakly notched bearing slender, plumose setae, basis broad, merus anterior margin expanded, overlapping carpus and propodus which are telescoped together; dactylus almost straight. Pereopods 5-6 short, carpus subconiform, with 2 distal spines and numerous posterior marginal denticles. Pereopods 5-7 dactylus with accessory tooth. Pereopod 7 elongate, basis anterior and posterior margins with long setae. Epimera rounded. Urosome reduced. Urosomite 2 free, produced ventrally into a rounded plate. Urosomite 3 and telson fused. Uropod 1 biramous, outer ramus over two thirds length of peduncle, inner ramus less than one third length of outer ramus. Uropod 2 absent. Uropod 3 composed of elongate slender peduncle only, which bears two distal setae. Telson evenly rounded, unarmed.

Remarks. This species does not readily fit the key to *Siphonoecetes* published by Just (1983). The absence of uropod 2 fits the key couplet leading to *Concholestes* and *Caribboecetes*, but the presence on the dactylus of pereopods 5-7 of an accessory tooth is incongruent and leads from the other half of the primary couplet to alternative taxa. If this latter character were ignored, the present species would key out to *Caribboecetes*. Just (1984) provided a key to this genus, but again difficulty is experienced in attempting to key the present taxon to the proximity of a sister-species. Couplet 1 of the key differentiates taxa with (a) antenna 2 longer than head and cephalon combined, and cephalon and first 3-5 pereonites with transverse rows of dorsal setules from (b) antenna 2 shorter than head and cephalon combined, and cephalon and pereon at most with scattered dorsal setules. Present material has antenna 2 equal to head and cephalon combined and lacks transverse setule rows. In general appearance it seem closest to the taxa with long antenna 2 and setule rows, especially *C. barbadensis*. It differs from that species in its rounded rostrum, less produced ocular lobes, more setiferous mandible palp article, shorter antenna 1 flagellum, toothed palm of gnathopod 1, accessory tooth on the dactylus of pereopods 5-7 and weakly spinous inner ramus of uropod 1. It seems most sensible to create a new genus for this species. *Polynesoecetes* appears to be closest to *Caribboecetes* but its true phylogenetic relations cannot be ascertained until further detailed analysis of the Siphonoecetinae is carried out (Just, personal communication).

Habitat. Unknown, but presumed like its congeners to live in the empty shells of a species of gastropod.

Distribution. Known only from the type locality.

Etymology. Named after the vessel *Keke* III which plies between Cook's Bay and Papeete.

ACKNOWLEDGEMENTS. I am grateful to Dr Jean Just for helpful comments concerning the new genus *Polynesoecetes*.

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APPENDIX 1

Station data

Station 1. Tahiti, Pte Urareva, 17°32'S 149°23'W, 21 Nov 1986, *Sargassum* from lagoon.
Station 2. Tahiti, Near Hitiaa, 17°36'S 149°17'W, 21 Nov 1986, *Sargassum* from lagoon.
Station 3. Tahiti, same locality and date, arborescent red alga from lagoon.
Station 4. Tahiti, same locality and date, *Padina* and coral rubble from lagoon.
Station 5. Huahine, 16°45'S 151°01'W, 26 Nov 1986, *Halimeda* and shell gravel from sheltered, silty inlet.
Station 6. Huahine, Lagon de Fare, 16°43'S 151°02'W, 27 Nov 1986, *Turbinaria ornata* from lagoon.
Station 7. Huahine, same locality and date, *Halimeda* from lagoon.
Station 8. Huahine, same locality and date, *Padina*-covered rocks from lagoon.
Station 9. Bora Bora, 1 km north of Paoaoa, 29 Nov 1986, *Turbinaria ornata* from sheltered lagoon.
Station 10. Bora Bora, same locality and date, *Padina* from lagoon.
Station 11. Bora Bora, Vaitape, 16°30'S 151°45.5'W, 29 Nov 1986, *Sargassum* from lagoon.
Station 12. Bora Bora, same locality and date, beach strand-line debris.
Station 13. Moorea, north-east entrance to Cook's Bay, 17°29'S 149°49.5'W, 2 Dec 1986, branching brown alga from lagoon.
Station 14. Moorea, same locality and date, *Halimeda* from lagoon.
Station 15. Moorea, same locality and date, coral rubble from lagoon.
Station 16. Moorea, same locality and date, *Padina* growing on a bank of sea-urchin spines.
Station 17. Moorea, near Ilot Tiahura, 17°29'S 149°54.5'W, 4 Dec 1986, *Sargassum* on inner side of barrier reef.
Station 18. Moorea, same locality and date, *Turbinaria ornata* from lagoon.
Station 19. Moorea, same locality and date, *Halimeda* from lagoon.
Station 20. Moorea, same locality and date, *Turbinaria ornata* with epiphytes in lagoon.
Station 21. Moorea, same locality and date, *Dictyota* in lagoon.
Station 22. Moorea, near Pte Faupo, 17°30'S 149°46'W, 9 Dec 1986, *Sargassum* on wave-planated reef crest unprotected by barrier reef.
Station 23. Moorea, north-east entrance to Cook's Bay, 17°29'S, 149°49'W, 11 Dec 1986, coral rubble from lagoon.
Station 24. Moorea, same locality and date, living *Pocillopora* from lagoon.
Station 25. Moorea, same locality and date, coral rock and *Porolithon* from lagoon.
Station 26. Moorea, same locality and date, *Padina*-covered rocks from lagoon.
Station 27. Moorea, same locality and date, *Padina* from jetty.
Station 28. Moorea, same locality and date, dead coral with epiphytes from lagoon.

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Revision of the New Guinean Genus *Mallomys* (Muridae:Rodentia), with Descriptions of Two New Species from Subalpine Habitats

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ABSTRACT. Four species of *Mallomys* are recognised: *M. rothschildi* Thomas, 1898, with the subspecies *M. r. weylandi* Rothschild & Dollman, 1932 (syn. *M. argentata* Rothschild & Dollman, 1932); *M. aroaensis* (De Vis, 1907) with the subspecies *M. a. hercules* Thomas, 1912; *M. istapantap* n.sp., and *M. gunung* n.sp. *Mallomys rothschildi* is the smallest species. It is distinguished from the others by its relatively and often absolutely longer tail, short, diamond-shaped interparietal, and small cranial dimensions. It is found above about 1,500 m along the New Guinean Central Cordillera but is absent in the extreme southeast. It nests primarily in tree hollows. The subspecies *M. r. weylandi* is morphologically much more variable than any other *Mallomys* taxon. This variability may be the result of the absence of congeners within its range. *Mallomys aroaensis* is intermediate in size. Externally it differs from *M. rothschildi* except some individuals of *M. r. weylandi* in its lighter, grey colour, with long white-tipped guard hairs, and an ill-defined dorsal stripe. Cranially, its broad rostrum, inflated frontals, and great bizygomatic width relative to toothrow length distinguish it from all other species of *Mallomys*. It is found only in Papua New Guinea at altitudes from 1,100 m to about 2,450-3,850 m along the Central Cordillera, and to 3,600 m on the Huon Peninsula. It nests primarily in burrows. *Mallomys istapantap* n.sp. is the largest species, and appears to be restricted to subalpine grasslands and the upper montane forest fringe at 2,450-3,850 m in the east-central part of the New Guinean Central Cordillera. It is readily distinguished from all other species of *Mallomys* by its pale ears, and from *M. rothschildi* and *M. aroaensis* by its large size, short tail, large hypsodont molars, and numerous other cranial features (see diagnoses). It also nests in burrows. *Mallomys gunung* n.sp.resembles *M. istapantap* n.sp. externally, but lacks the pale ears of that species and differs markedly in cranial morphology (see diagnosis). Thus far it is known only from the western part of the Central Cordillera, from Mount Carstenz to Mount Wilhelmina, at altitudes of between 3,500 and 4,050 m.

FLANNERY, T.F., K. APLIN, C.P. GROVES & M. ADAMS, 1989. Revision of the New Guinean genus *Mallomys* (Muridae: Rodentia), with descriptions of two new species from subalpine habitats. Records of the Australian Museum 41(1): 89-111.

Species of the genus *Mallomys* are among the very largest of living murids. They are shaggy coated, herbivorous rats found only above 1,000 m along New Guinea's Central Cordillera and Huon Peninsula. Now recognised as part of the New Guinean "old endemic" radiation (Tate, 1951), their precise relationships with other genera remain unclear.

The taxonomy of the species of *Mallomys* has long been contentious. During the late nineteenth and early twentieth centuries a number of species names were proposed, all of which have been regarded more recently as referring to a single variable species. Thomas (1898) based *Mallomys rothschildi* upon a single very dark animal from between Mounts Musgrave and Scratchley in south-eastern New Guinea. In 1912 he proposed a second name, *M. hercules,* for a large, greyish animal from the Huon Peninsula. Unknown to Thomas, Charles De Vis of the Queensland Museum had in 1907 decribed and named a large grey murid *Dendrosminthus aroaensis.* This specimen came from the head of the Aroa River in south-eastern New Guinea. De Vis clearly had misgivings about naming this animal, as he wrote "...I feel hardly justified in running the risk of perpetrating a synonym, otherwise I should propose for it the name *Dendrosminthus aroaensis...*" (1907, p.11). Although such a "conditional name" would be unavailable were it proposed after 1961, prior to that date this does not prevent availability (see the Code, Art.15). Two additional taxa were described by Lord Walter Rothschild and Guy Dollman in 1932. They recognised both a blackish species (*M. weylandi*) and a grey one (*M. argentata*) from the Weyland Range in western New Guinea.

There matters rested until Rümmler (1938) reviewed the taxonomy of all of the New Guinean murids. He recognised but a single species of *Mallomys,* with three geographical subspecies: *M. r. rothschildi* from south-eastern New Guinea, *M. r. hercules* from the Bismarck Range and Huon Peninsula, and *M. r. weylandi* from the Weyland and Snow Mountains. Tate (1951), in his revision of the New Guinean murids, tentatively maintained Rümmler's three subspecies, but felt that *M. r. weylandi* and *M. r. rothschildi* were very similar, and only doubtfully distinct. He had examined both black and grey furred animals from the Bele River area of Irian Jaya, and had determined that these were simply colour morphs within a single species. Laurie (1952) and Laurie & Hill (1954) also recognised only a single species of *Mallomys* although Laurie (1952) had also noted the existence of both black and grey animals in collections from various parts of Papua New Guinea.

No further revisionary work was undertaken on the genus until this study. However, there were several indications from field workers that Rümmler's solution was not the correct one. Menzies & Dennis (1979), for example, mention that some native peoples from the central highlands of Papua New Guinea recognised two kinds of *Mallomys.* Various social anthropologists and geographers (e.g. P. Dwyer, D. Hyndman, G. Hope, personal communication) have noticed a similar situation when collecting folk taxonomies and undertaking other work.

Our work on this problem began with the collection by two of us (T.F., K.A.) of *Mallomys* material, including tissues suitable for electrophoresis, from various localities throughout Papua New Guinea during 1981-1986. We had also noted considerable variation within available study material, and had tentatively recognised two species on the basis of cranial and external morphology. Electrophoretic results suggested that three groups could be recognised within our material from Papua New Guinea. This view was substantiated by a thorough examination of all relevant materials, and was extended through the recognition of a fourth species from Irian Jaya based on morphological criteria alone. Armed with this reappraisal of all *Mallomys* material held in Australian institutions, one of us (C.P.G.) travelled to London to examine type and other material held in the British Museum, and sought material in other European museums as well. We afterwards borrowed extensively from the holdings of *Mallomys* in the American Museum of Natural History.

The descriptions of the two new taxa proposed in this work were prepared by Flannery, Aplin and Groves, and only those authors should be cited as authorities for the names.

Materials and Methods

External measurements used in this study were taken from museum labels. In most cases they are known to have been taken on freshly dead individuals. Cranial measurements follow Musser (1970), except for toothrow length, which here has been taken as maximum crown length (rather than alveolar length). Colour nomenclature where capitalised follows Ridgway (1886).

Abbreviations are as follows: B.M. - British Museum (Natural History) mammal specimen. AM M - Australian Museum mammal specimen, AM F - Australian Museum fossil specimen. AMNH - American Museum of Natural History mammal specimen, CM - Australian National Wildlife Collection specimen. RM - Rijksmuseum van Natuurlijke Historie [Leiden] mammal specimen.

Results

Electrophoresis. Specimens of *Mallomys* sampled for electrophoretic analysis are listed in Table 1. Unfortunately, the sample size is small, as many *Mallomys* were received in the field long after death and their tissues had commenced to decay. Elsewhere it has been shown that only a few

animals per population are needed to characterise that population for systematic purposes using allozyme electrophoresis (Richardson *et al.*, 1986, Gorman & Renzi, 1979, Adams *et al.*, 1987).

A total of 39 loci allowed for reliable genetic interpretation in the present study. The enzymes and proteins used are listed in Appendix 1 and Table 2 shows the allelic profiles of the three populations for the 39 loci. A matrix of genetic distances between populations, using both fixed differences (see Richardson *et al.*, 1986) and corrected Nei Distances (Nei Ds, see Nei, 1978) is given in Table 3. The single specimen from Mount Albert Edward (population A, representing *M. istapantap* n.sp.) differed from the other two populations sampled at an average of 33% of its loci (Nei D = 0.38). The Mount Sisa sample (population B, representing *M. aroaensis*) differed from the Telefomin sample (population C, representing *M. rothschildi*), at 15% of loci examined (Nei D = 0.25).

Even in the absence of other data, a good case can be made on the basis of electrophoresis alone that the Mount Albert Edward specimen represents a distinct species. The level of difference encountered far exceeds that expected for allopatric populations of a single species (typically 0 to 10%, see Richardson *et al.*, 1986). Unfortunately, the *M. rothschildi* and *M. aroaensis* comparison involves two localities 150 km apart. These two allopatric populations exhibit genetic differences greater than are expected for a single species and greater than have been thus far encountered for other species of New Guinean mammals (Adams, unpublished). Nevertheless, the level of difference is by itself not sufficient to characterise two species, as it is not possible to rule out within-species geographic variation. Fortunately, the morphological data indicate extensive sympatry of the two species and the 15% fixed genetic differences encountered here would if found in sympatry, be sufficient to unequivocally characterise the two species.

Morphology. Large samples of *Mallomys rothschildi* (N = 48) and *M. aroaensis*, (N = 72) as well as moderate samples of *M. istapantap* n.sp. (N = 20) and *M. gunung* n.sp. (N = 8) (Appendix 2), were available for this analysis. Several non-metric as well as metric differences in the

Table 1. Details of specimens used in the electrophoretic analysis.

Population	Species	Locality	Specimen no.
A	*M. istapantap* n.sp.	Mount Albert Edward, Central Province	AM M12875
B	*M. aroaensis*	Bobole Village Mount Sisa, Southern Highlands Province	AM M16693, AM M17096, AM M17893, AM M17894
C	*M. rothschildi*	Telefomin area West Sepik Province	AM M13730, AM M15999, AM M17361, AM M17362

Table 2. Allele frequencies at the 39 loci examined. Locus and Allele designation follow Adams *et al.*, 1987. 2N is the number of haploid genomes sampled.

Locus	A (2N)->(2)	B (8)	C (8)
Acon-2	c	b (75)	b
		a (25)	
Adh-1	a	a	b
Adh-2	-	b	a
Ak-1	a	a	b (50)
			a (50)
Ak-2	c	b	b (13)
			a (87)
Dia	b	a	a
Enol	a	a	b
Gapd	-	a	a
Got-2	a	b	b
G6pd	b	a	b

Locus	A (2N)->(2)	B (8)	C (8)
Gpd	a	b (50)	b (25)
		a (50)	a (75)
Idh-2	b	a	a
Ldh-1	a	b	b
Mpi	b	a	a
Pep-A	b	a	b
Pep-D	b	a	a
6Pgd	a	b	b (25)
			a (75)
Pgm-1	a	b	a
Pgm-2	b	a	a
Pk-2	a	b (25)	a
		a (75)	

The following loci were invariant: *Acon-1, Acp, Ada, Ca, Fdpase, Got-1, Gpi, Idh-1, Lap, Ldh-2, Mdh-1, Mdh-2, Np, Pep-B, Pep-C, Pgk, Pk-1, Sod, Sordh.*

Table 3. Matrix of genetic differences between the three populations of *Mallomys*. Lower matrix - percentage fixed differences; upper matrix - Nei D's.

	A	B	C
A	-	0.45	0.37
B	35	-	0.23
C	30	14	-

external morphology and cranium were noted between these taxa.

Pelage and external morphology. Pelage and skin differences allow for identification of all four taxa. The overall dorsal colouration of most *M. rothschildi* is black or very dark brown, with a paler underfur. Where the fur is parted to reveal the underfur (e.g. around the ears in study skins) a pale grey or white flash appears to be present. The guard hairs are usually uniformly black. Almost all *M. rothschildi* have some dark fur on the venter, a feature never seen in other species, and in *M. r. rothschildi* the entire venter is grey interspersed with dark guard hairs (unique in the genus). The ears are black, and the tail is long relative to that of other *Mallomys* (Table 4). Within Papua New Guinea, *M. r. rothschildi* is readily distinguished from *M. aroaensis* and *M. istapantap* n.sp. by its dark dorsal colouration, lack of pale tips on the guard hairs and grey venter. *Mallomys rothschildi weylandi*, however, is polymorphic in colouration. Many individuals are similar in dorsal colouration to *M. r. rothschildi*, but a few are dark grey with light-tipped guard hairs and possess a dark dorsal stripe as in *M. aroaensis*. These differ from all *M. aroaensis* however in having the underfur of the dorsum a darker shade of grey, and (all except one specimen) in having grey patches of fur in the inguinal region.

Mallomys aroaensis, *M. gunung* n.sp. and *M. istapantap* n.sp. differ from most *M. rothschildi* in having an overall greyish rather than black appearance. They also appear "frosted" due to the white tips of the darkish guard hairs. The contrast with the underfur is not as great as in *M. rothschildi*. All have pure white venters, which lack guard hairs. *Mallomys aroaensis* differs from *M. istapantap* n.sp. and *M. gunung* n.sp. in possessing an ill-defined dorsal stripe, which is due to a darkening of the tips of the underfur (but no change in the guard hairs), and a longer tail (Table 4). In some individuals (particularly in the subspecies *M. a. hercules*) the dorsal stripe is broken up into a series of irregular blotches, but some midline darkening is invariably present. Such a feature is never seen in *M. istapantap* n.sp. and *M. gunung* n.sp.

The lighter (flesh coloured) ears of *M. istapantap* n.sp. are of great diagnostic value, the ears of all other species being dark.

Mallomys gunung n.sp. is similar to *M. istapantap* n.sp. in its large size, lack of a dorsal stripe and short tail. It differs however in its darker ears, slightly lighter grey

Table 4. External measurements in mm and gms for the species of *Mallomys*. HB = head body length, TV = tail-vent length, HF = hindfoot length (su), E = ear (notch) length. X = mean, R = range, N = sample size, STD = standard deviation. Samples include all BM, AM and CM specimens (except juveniles) for which measurements taken in the flesh exist.

		HB	TV	HF	E	WT
Mallomys istapantap n.sp	X	397.1	338	70.3	30.9	1,950
	R	352-477	280-363	60-80	23-37	1,950
	N	12	11	11	12	1
	STD	32.09	24.86	5.93	3.80	-
Mallomys gunung n.sp.	X	418	366	75	35	-
	N	1	1	1	1	-
Mallomys a. aroaensis	X	366	372	69.8	28.8	1,530
	R	292-410	295-420	64.4-76.0	25.3-33.0	1,410-1,710
	N	45	45	44	43	4
	STD	24.5	30.2	2.80	1.84	127.3
Mallomys a. hercules	X	-	-	67.0	25.5	-
	R	-	-	67-67	25-26	-
	N	-	-	2	2	-
Mallomys r. rothschildi	X	366	380.2	69.1	29.3	1,134
	R	306-405	337-423	63.0-80.0	26.0-31.0	925-1,500
	N	27	27	26	26	7
	STD	19.91	22.36	3.83	1.17	203
Mallomys r. weylandi	X	387	402	71.1	26.0	-
	R	350-440	377-440	66-75	17-29	-
	N	9	9	9	9	-
	STD	27.21	19.02	2.76	3.87	-

dorsal colouration which lacks a brownish suffusion, and extremely long claws.

Overall size is also a valuable feature in distinguishing the four taxa. Adult *M. rothschildi* weigh between 925 and 1,500 g, *M. aroaensis* between 1,410 and 1,710 g, and *M. istapantap* n.sp. about 1,950 g. No weights are available for *M. gunung* n.sp., but it is probably slightly smaller than *M. istapantap* n.sp. The values for head plus body length and the skull measurements confirm that *M. rothschildi* is the smallest species, *M. aroaensis* next, and the two high-mountain species largest.

Skull and teeth. We have been able to find no consistent differences in molar cusp patterns between the four *Mallomys* species, although there are differences in size and the degree of hypsodonty. *Mallomys istapantap* n.sp. and *M. gunung* n.sp. have much larger molars (Table 5), which are much more hypsodont than in other species of *Mallomys* (Fig. 1). Major non-metric cranial differences distinguish *M. istapantap* n.sp. from the other species. The premaxillary/maxillary suture of *M. istapantap* n.sp. is more sinuous, with a dorsal and ventral anterior projection of the maxilla (Fig. 2). In the remaining species the ventral projection is absent, the suture running gently posteriorly towards the incisive foramen. The bony palate in both the high-mountain species (*M. gunung* n.sp. and *M. istapantap* n.sp.) is grossly thickened dorsoventrally. That of *M. istapantap* n.sp. slopes gently posteriorly, and unites at an acute angle with the upwardly sloping ventral surface of the mesopterygoid fossa, while in *M. gunung* n.sp. (as in the other species of *Mallomys*) the posterior edge of the bony palate slopes sharply towards the mesopterygoid fossa, intersecting it at a less acute angle (Fig. 2). The mesopterygoid fossa of *M. istapantap* n.sp. differs from that of other taxa in that internally it is strongly elliptical, rather than round (Fig. 2). The orbital region differs from that of the other three species in that the sphenopalatine foramen is slit-like and partly hidden by the maxilla rather than ovoid and readily visible (Fig. 2). In the basicranial region *M. istapantap* n.sp. differs from its congeners in that the alisphenoid makes a much larger contribution to the anterior margin of the postglenoid vacuity than in the remaining species, and that the postglenoid vacuity itself is somewhat different in shape, its anterior edge being less vertically inclined (Fig. 2).

The cranium of *M. aroaensis* differs from that of other *Mallomys* species in having a relatively more inflated rostrum (Fig. 3), as well as inflation of the dorsal part of the maxillary facial lamina.

The cranium of *Mallomys r. rothschildi* differs from that of the other *Mallomys* species in its narrower interorbital region (Table 5), narrower bizygomatic breadth (Table 5), in its anteroposteriorly short, diamond-shaped interparietal (Fig. 4), and in its overall smaller size. *Mallomys rothschildi weylandi* is similar in most cranial dimensions to *M. r. rothschildi*, but the interparietal is more variable in shape, the interorbital width and palatal length are greater, and the molars are smaller (Table 5).

The cranium of *Mallomys gunung* n.sp. differs markedly from that of other *Mallomys* species in the construction of the rostrum. The nasals and dorsal section of the premaxillae are foreshortened, giving the upper incisors the markedly proödont appearance remarked upon by Tate (1951). The incisor enamel is pale yellow, being less strongly pigmented than in all other *Mallomys* species except some high altitude individuals of *M. rothschildi*.

Systematics

Mallomys Thomas, 1898

Type species. *Mallomys rothschildi* Thomas, 1898 (p.2), based upon BM No 97.12.6.6., adult male skin (mounted) and skull from the Owen Stanley Range, between Mount Musgrave (8°55'S, 147°22'E) and Mount Scratchley (8°45'S, 147°29'E), 1,500-1,800 m.

Included species and distributions. *Mallomys rothschildi:* the New Guinean Central Cordillera, from the Weyland Range in the west to the Owen Stanley Range in the east, at altitudes of 1,500 to 3,700 m. Including the subspecies *M. r. rothschildi* (Owen Stanley Range to Telefomin, P.N.G.), and *M. r. weylandi* (Weyland Range to Mount Wilhelmina area, Irian Jaya) (Fig. 5).

Mallomys aroaensis: the eastern part of the New Guinean Central Cordillera, from Mount Sisa in the west to Mount Simpson in the east, at altitudes from 1,100 to 2,450 m; also the Huon Peninsula to 3,600 m (Fig. 6). Including the subspecies *M. a. aroaensis* (Mount Sisa to Owen Stanley Range), and *M. a. hercules* (Huon Peninsula).

Mallomys istapantap n.sp.: the east-central part of the New Guinean Central Cordillera, from Mount Giluwe in the west to Mount Victoria in the east, in subalpine herbfields and forest margins above 2,450 m to at least 3,850 m, and possibly to the limit of vegetation (Fig. 7).

Mallomys gunung n.sp.: from the Snow Mountains to Mount Wilhelmina, Irian Jaya, at altitudes of 3,500 to 4050 m, and possibly to the limit of vegetation (Fig. 7).

Generic diagnosis. Musser (1981) has shown that the species of *Mallomys* lack many derived cranial features seen in large murids with similar molar morphology that are found on islands to the west of New Guinea. He suggests that the species of *Mallomys* are part of a primitive group of murids not closely related to these Asian taxa. His work should be referred to for diagnostic features distinguishing New Guinean from Asian murids. Within New Guinea the species of *Mallomys* can be distinguished from all other murids by possessing the following combination of features: size large (weight between 1 and 2 kg when adult); coat long and dense, somewhat woolly, with long guard hairs projecting from the underfur; mammary formula is 1 + 2 = 6; molars complex, cusps forming "trilobed" pattern on upper molars; palate greatly thickened.

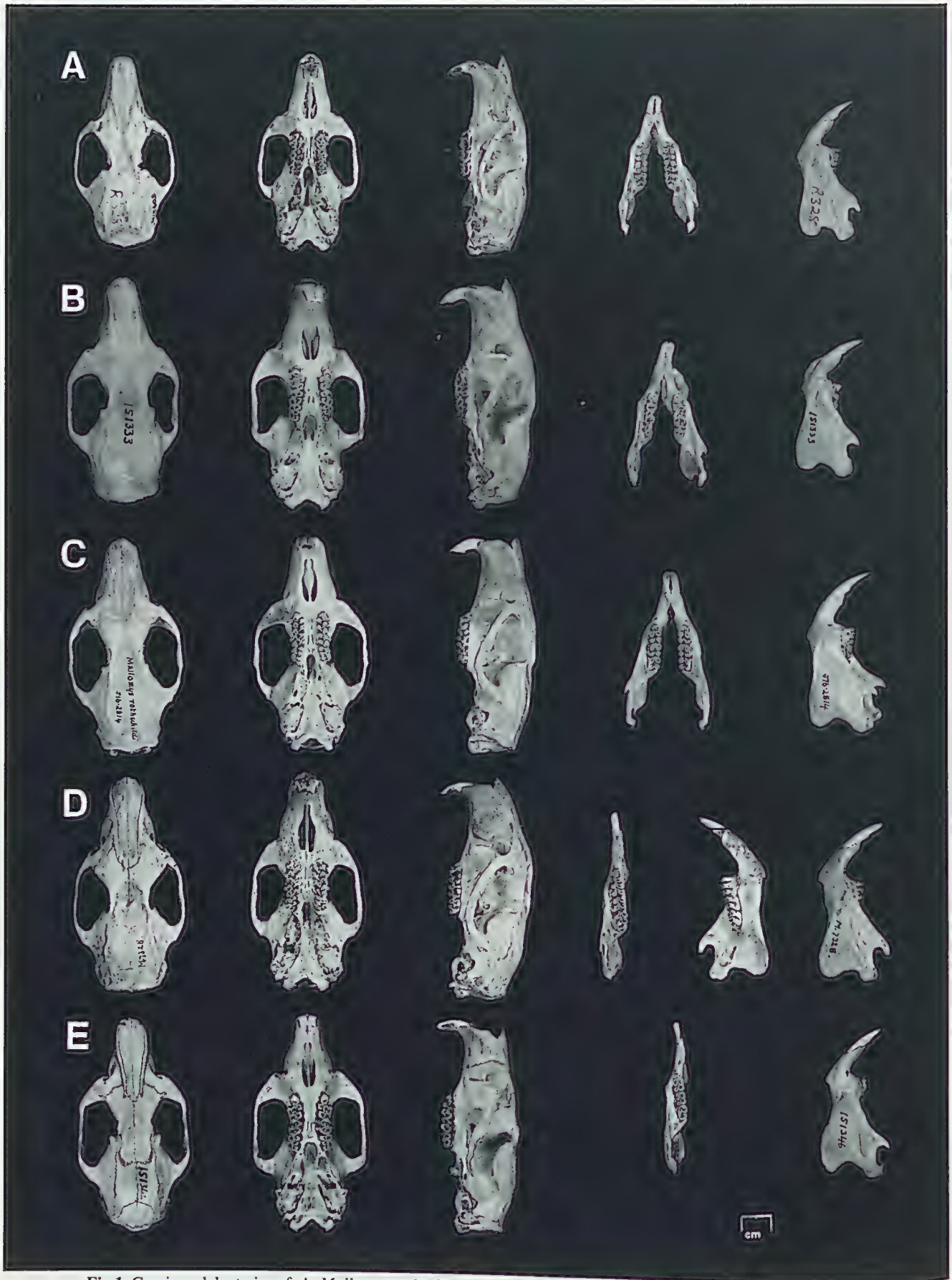

Fig.1. Crania and dentaries of: A, *Mallomys rothschildi rothschildi* AM M15603; B, *Mallomys rothschildi weylandi* AMNH15133; C, *Mallomys aroaensis* holotype QM J2814; D, *Mallomys istapantap* n.sp. holotype AM M7328; and E, *Mallomys gunung* n.sp. holotype AMNH151346.

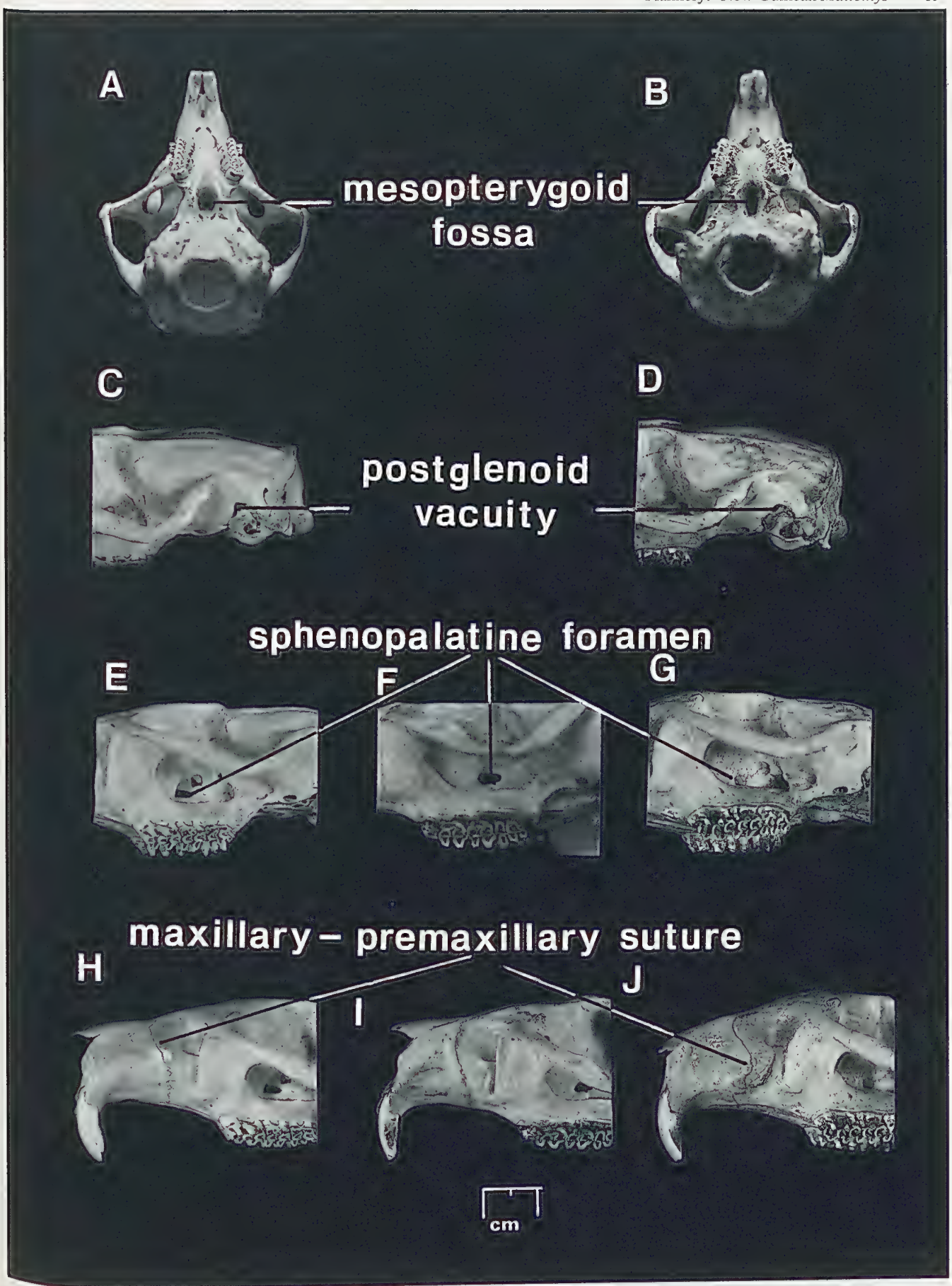

Fig.2. Comparison of the mesopterygoid fossa, postglenoid vacuity, sphenopalatine foramen and maxillary/premaxillary suture, in the holotypes of *Mallomys istapantap* n.sp. (B,D,G,J), *Mallomys gunung* n.sp. (F,I) and *Mallomys aroaensis* (A,C,E,H).

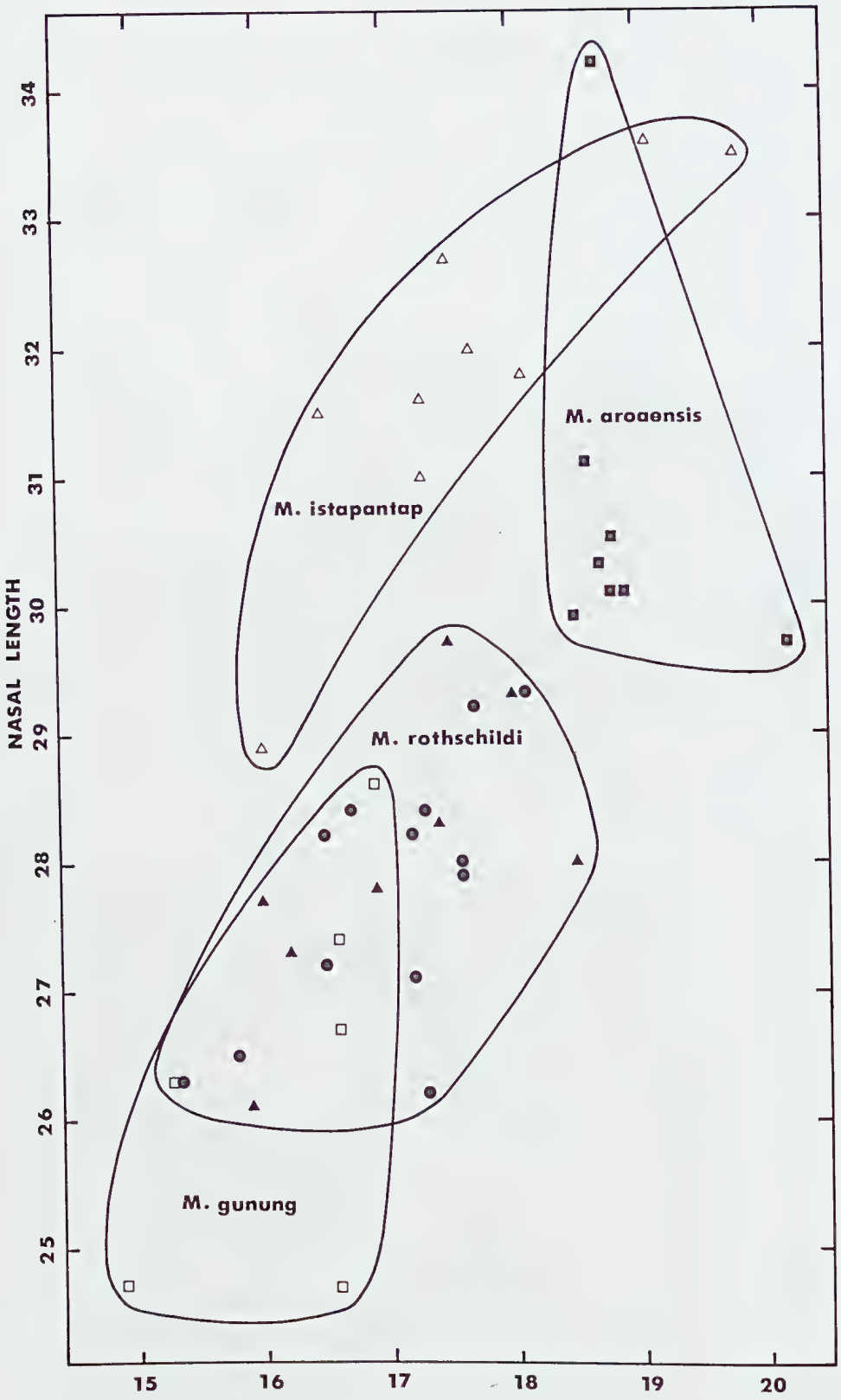

Fig.3. Bivariate plot of nasal length over rostrum width for the four species of *Mallomys* (the dots are *M. r. rothschildi* and the solid triangles are *M. r. weylandi*) (adults only).

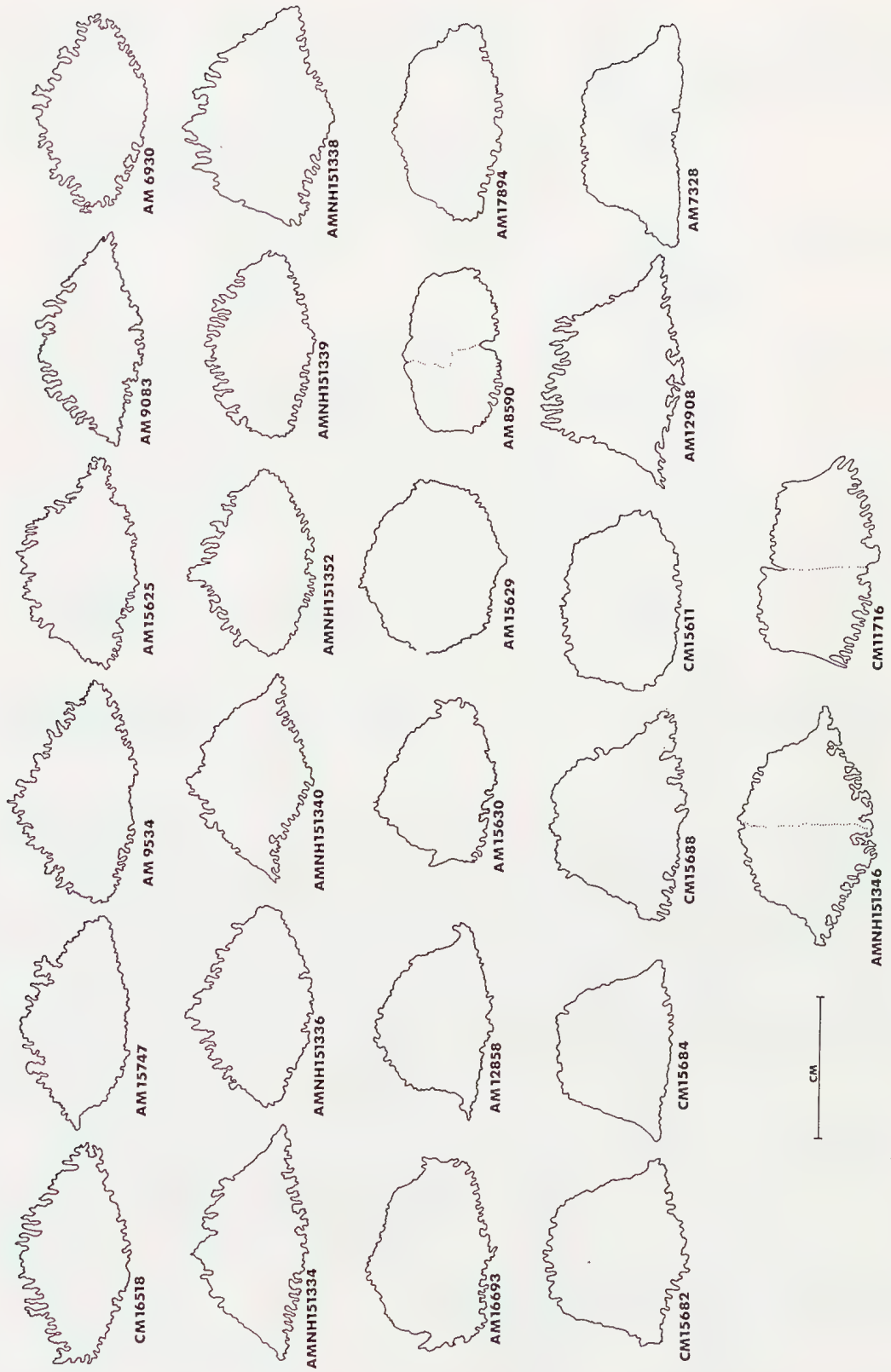

Fig.4. The interparietals of *Mallomys rothschildi rothschildi* (left column), *M. r. weylandi* (second (left) column), *Mallomys aroaensis aroaensis* (middle column), *Mallomys istapantap* n.sp. (fourth (right) column) and *Mallomys gunung* n.sp. (right column). Except for *M. gunung* n.sp. (where only three complete crania are known), the most common morphologies are towards the bottom of the page, the highly unusual ones at the top.

Table 5. Cranial and dental measurements for the species of *Mallomys* (from specimens held in the AM, QM, RMNH, BM(NH) and CM and borrowed from AMNH. Includes some subadults).

		Mallomys istapantap n.sp.	*Mallomys gunung* n.sp.	*Mallomys aroaensis aroaensis*	*Mallomys aroaensis hercules*	*Mallomys rothschildi rothschildi*	*Mallomys rothschildi weylandi*
Condylobasal length	X	76.9	74.9	72.8	74.8	72.1	72.2
	R	75.0-80.6	72.1-77.2	70.2-75.7	74.5-75	68.3-74.6	69.5-75.4
	N	9	3	9	2	13	10
	STD	2.06	2.60	1.89	-	1.85	2.04
Bizygomatic width	X	41.3	40.6	39.3	40.3	38.1	37.5
	R	39.9-42.3	40.2-41.0	36.8-42.4	39-41.3	36.0-39.3	36.0-39.2
	N	9	3	10	4	16	10
	STD	1.03	-	2.23	1.04	1.08	1.11
Palatal length	X	39.9	40.3	36.4	-	35.7	39.7
	R	36.2-42.3	39.3-41.6	34.5-38.6	-	34.0-37.6	35.1-41.9
	N	9	6	10	-	16	8
	STD	1.88	.94	1.43	-	1.05	2.77
Nasal length	X	31.8	26.4	31.0	30.3	27.5	27.9
	R	28.9-33.6	24.7-28.6	26.8-34.2	29-31.5	26.5-29.3	26.1-29.7
	N	9	6	10	4	15	9
	STD	1.42	1.53	2.56	0.87	1.26	1.11
Incisive foramen length	X	15.5	13.7	14.6	15.3	13.7	15.4
	R	14.0-17.2	11.6-14.9	13.6-17.1	14.6-16	12.7-15.0	13.9-15.9
	N	9	6	10	2	17	10
	STD	1.00	1.32	1.15	-	.72	.77
Rostrum breadth at zygomatic plates	X	17.7	16.2	18.8	-	17.0	17.1
	R	16.0-19.8	15.3-16.9	16.5-22.1	-	15.3-18.1	15.9-18.5
	N	9	6	10	-	14	8
	STD	1.18	.83	1.35	-	.77	.96
Maximum nasal width	X	10.3	9.6	9.9	12.4	8.8	9.0
	R	9.4-11.1	9.4-9.8	8.2-10.8	11-13.5	8.0-10.4	8.0-9.6
	N	9	5	10	4	15	10
	STD	.57	.16	.88	1.11	.60	.48
Interorbital width	X	11.2	11.0	10.9	12.2	9.4	10.5
	R	8.8-13.3	10-11.3	9.2-12.3	11-13	8.2-11.1	9.7-11.0
	N	8	5	10	5	16	10
	STD	1.59	.54	1.16	.84	.08	.76
M1-3/ length	X	18.4	18.8	17.0	17.0	17.2	16.5
	R	17.4-19.1	17.4-20	16.3-18.0	16.2-18	15.8-18.2	15.7-17.5
	N	8	5	10	6	18	11
	STD	.57	.96	.67	.57	.64	.21
M1/ length	X	8.9	9.2	8.4	-	8.4	7.9
	R	8.4-9.3	8.1-10.1	7.4-9.9	-	7.7-9.3	7.8-8.7
	N	9	4	10	-	16	9
	STD	.33	.94	.72	-	.39	.42
M1/ width	X	5.4	5.8	5.2	-	5.3	5.2
	R	5.0-6.0	5.6-6.0	4.9-5.4	-	5.2-5.6	5.1-5.4
	N	8	4	10	-	16	9
	STD	.35	.18	.13	-	.12	.11

Fig.5. Distribution of *Mallomys rothschildi*. Solid dot and star = *M. r. rothschildi*, open circle and star = *M. r. weylandi*, star = type locality.

Mallomys rothschildi Thomas, 1898

Revised diagnosis. All except some individuals of *M. r. weylandi* are distinguishable externally from other species by their much darker dorsal colouration. Contour hairs silvery at base with long black tips; the guard hairs of the midback are uniformly dark (rather than light tipped), and the venter almost always includes some greyish or black hairs. In all *M. rothschildi* the tail is relatively and often absolutely longer than in the other taxa; the depigmented terminal zone extends over two thirds to three quarters of the total tail length; and the tail scales overlap less than in other species, so that the tail surface is smoother, less rasping. In terms of body weight it is the smallest *Mallomys* (Table 4). The cranium can usually be distinguished from that of other species of *Mallomys* by its broad, short and more or less diamond shaped rather than hemidiscoidal interparietal (Fig. 4) and its relatively narrower bizygomatic width (Table 5).

Mallomys rothschildi rothschildi Thomas, 1898

Mallomys rothschildi Thomas, 1898: 2.

Type material. Holotype: BM 97.12.6.6 adult male skin and skull with dentaries. From between Mounts Musgrave and Scratchley (8°45'S, 147°29'E), 1,500-1,800 m.

Diagnosis. Invariably blackish dorsally with all black guard hairs. Venter invariably entirely dirty grey with presence of many black guard hairs, rather than largely pure white and lacking guard hairs as in *M. r. weylandi* . Tail scales smaller, usually 9-11 per centimetre of length (in 16 out of 17 skins examined) as opposed to 7-8 in *M. r. weylandi*. Interparietal usually more diamond shaped (Fig. 4), interorbital width usually narrower (Fig. 8), and toothrow length often greater (Table 5).

Mallomys rothschildi weylandi Rothschild & Dollman, 1932

Mallomys weylandi Rothschild & Dollman, 1932: 212.

Type material. Holotype: BM 1939.1943 (previously F.S.M. No 95) adult female skin with skull and dentaries. From The Gebroeders, Weyland Range (3°38'S, 133°55'E), Irian Jaya, 2,100 m.

Synonyms. *Mallomys argentata* Rothschild & Dollman, 1932 (p.212). Based upon the syntypes BM1939.1942 (previously F.S.M. 91) and BM 33.6.1.33, adult female skins and skulls from The Gebroeders, Weyland Range (3°38'S, 133°55'E) Irian Jaya, between 2,150 and 2,450 m.

Diagnosis. Either blackish dorsally with black guard hairs or greyish with pale tipped guard hairs. Ventrally white, but almost always with small patches of greyish fur (often with black guard hairs) in inguinal region. Interorbital width (Fig. 8) and palatal length usually greater than in *M. r. rothschildi,* but toothrow often smaller (Table 5). Only 7-8 scales per cm of tail length as opposed to 9-11 in *M. r. rothschildi.*

Discussion. *Range. Mallomys rothschildi* seems to be confined to the western and central sections of the New Guinean Central Cordillera. There are two distinct subspecies. *Mallomys rothschildi weylandi* is found from the Weyland Range in the west to Mount Wilhelmina in the east, while *Mallomys rothschildi rothschildi* occurs from Telefomin in the west to between Mounts Musgrave and Scratchley in the east. The record of the holotype is far to the east of all other records, and it is only to the west of Morobe Province that the species appears to be common. At some localities (e.g. Telefomin, Mount Erimbari) it is caught to the exclusion of other *Mallomys* species. It also seems to be very common in the Mount Hagen area (Laurie, 1952; AM M specimens). At present, a gap of some 330 km (between Mount Wilhelmina and Telefomin) separates the distinctive subspecies *M. r. weylandi* and *M. r. rothshildi.* Investigation of this area should show whether these subspecies abut or intergrade. As presently understood, their morphology gives no indication of any intergradation, so that if this does occur, the intergrade zone is probably a narrow one. The altitudinal range of *M. rothschildi* is poorly known. In the Telefomin area it occurs as low as 1,500 m while on Mount Giluwe it occurs as high as 3,700 m, where it is sympatric with *M. istapantap* n.sp. Throughout the range of *M. r. rothschildi* it is frequently sympatric with *M. aroaensis,* although, as noted above, one or the other species may tend to dominate at any one locality.

Morphological variation. The degree of morphological variability is far greater in *M. r. weylandi* than in *M. r. rothschildi.* Although our sample of *M. r. weylandi* is small it includes remarkable variation in coat colouration and a more limited cranial variability. Overall, this sample shows the greatest variability of any *Mallomys* subspecies. The sample of ten skins studied by us includes five specimens which are indistinguishable in dorsal colouration from *M. r. rothschildi,* and five resembling *M. aroaensis* (Figs 9--10). Ventrally, all except one specimen are almost all white, with small patches of greyish hairs inguinally. The exception lacks the grey inguinal patches. Many individuals have readily visible dark guard hairs in these patches. Two of the blackish and two of the greyish individuals possess a white band encircling the middle of the body. This feature is seen rarely in *M. r. rothschildi,* and never in other species of *Mallomys.* Cranially, *M. r. weylandi* shows considerable variation in the shape of the interparietal. In *M. r. rothschildi* it is almost always diamond shaped and anteroposteriorly short. In *M. r. weylandi* most specimens are like this, but a few are similar to the more arched interparietal common in *M. aroaensis* (see Fig. 4).

We have examined the syntypes of *M. argentata* Rothschild & Dollman, 1932, and cannot distinguish them from any other *M. r. weylandi* on the basis of cranial morphology. In coat colour they are indistinguishable from the lighter coat colour morph present in the *M. r. weylandi* sample from the Bele River. Thus, we are confident that *M. argentata* is a synonym of *M. r. weylandi* Rothschild & Dollman, 1932.

There is little variation within *M. r. rothschildi.* Only two of the 20 British Museum skins and none of the five Australian Museum skins from the central highlands possess a striking white band on either side of the body, reaching from the whitish ventral zone up towards (but not onto) the mid-dorsal region; a third skin has the band on the left side only. However, two of the four Australian Museum specimens from Telefomin possess similar bands. Most specimens have inconspicuous white patches in front of the ears; the types of *M. r. weylandi* and of *M. r. rothschildi* lack them. A specimen (B.M.69.338) from the Schrader Mountains, above Kaironk, at about 1700 m, is larger than other specimens, and is unique in that the tail is shorter than the head plus body. The degree of blackening of the whitish ventral zone varies: in some it is so extensive that the underside looks nearly black, while in others it is pale grey. Finally, some specimens from very high altitudes (e.g. CM 16518 from Mount Wilhelm) have white incisor enamel.

Differences in the degree of morphological variability between subspecies exist in other New Guinean mammals. Flannery & Calaby (1987) discuss the case of *Spilocuscus maculatus. Spilocuscus m. goldiei* inhabits southern New Guinea, where it has no congeners. It exhibits great cranial variability. *Spilocuscus m. maculatus* is found in northern New Guinea, where it is sympatric with *Spilocuscus rufoniger.* Cranial variability is much less in *S. m. maculatus* and *S. rufoniger* than in *S. m. goldiei.* Indeed, in some features where two distinct states are found in *S. m. goldiei* (e.g. presence of frontal/maxillary or lachrymal/nasal suture, sometimes on opposite sides of a single skull), one condition (frontal/maxillary suture) is invariably found in *S. rufoniger* and the other (nasal/lachrymal suture) in *S. m. maculatus.* Flannery & Calaby suggest that this loss of variability in the taxa existing sympatrically may be due character displacement owing to interspecific competition, and concomittant changes in skull shape.

The situation seen in the subspecies of *M. rothschildi* and in *M. aroaensis* is strikingly similar to that in the species of *Spilocuscus.* In *M. r. weylandi,* which occurs in the absence of congeners, there is a range of morphological variation that in part encompasses that seen in both *M. r. rothschildi* and *M. aroaensis* which are sympatric in eastern New Guinea. Thus, our findings suggest that sympatry among congeners has the potential to reduce the range of morphological variation present in a taxon. Although the ecology of the species of *Spilocuscus* and *Mallomys* remains entirely unstudied, we consider it possible that this is due to character displacement owing to competitive interaction.

Reproduction and nest sites. A lactating female was

taken on 25 July 1972 on Mount Erimbari, and a suckling young (WT = 148 g) on 10 July 1985 in the Telefomin area. Almost all specimens of this species for which data exist were taken from tree hollows, or were shot at night in the canopy. The only exception that we know of is AM M15999, a young animal that was taken from deep in a limestone cave at 1,500 m in the Telefomin area. Interestingly, other *Mallomys* species have not been recorded for the Telefomin area.

Mallomys aroaensis (De Vis, 1907)

Dendrosminthus aroaensis De Vis, 1907: 11.

Type material. Holotype: QM J2814, male study skin and skull with dentaries collected at the head of the Aroa River (9°05'S, 146°48'E), Papua New Guinea.

Diagnosis. *Mallomys aroaensis* differs from all other *Mallomys* species in possessing the following combination of characters: usually relatively broader rostrum and more inflated frontal region; depigmented region of tail extending over only one half to two thirds length of tail (usually longer in other species), usually 7 or 8 scales per cm of tail length (only 1 skin in 33 studied did not, having 9), as opposed to 9 or more in *M. gunung* n.sp. and *M. r. rothschildi,* and 8-9 in *M. istapantap* n.sp. Differs from *M. rothschildi* in longer nasals (Fig. 3), shorter tail, pure white venter (rare in *M. rothschildi*) and lighter coloured dorsal underfur. Differs from *M. istapantap* n.sp. and *M. gunung* n.sp. in considerably smaller size, in possessing poorly-defined, dark dorsal stripe, has longer tail, smaller molars and thinner bony palate. Differs from *M. istapantap* n.sp. in darker ears, shape of posterior of bony palate, mesopterygoid fossa and postglenoid vacuity (Fig. 2). Differs from *M. gunung* n.sp in darker incisor enamel, and unretracted nasals and premaxillae.

Mallomys aroaensis aroaensis De Vis, 1907

Diagnosis. Lacking extreme inflation of frontals and rostrum seen in *M. a. hercules;* dorsal colour greyer, with more marked frosting (due to better expressed banding on hairs); mid-dorsal darkening better expressed.

Mallomys aroaensis hercules (Thomas, 1912)

Mallomys hercules Thomas, 1912: 19.

Type material. Holotype: BM 12.1.31.1, adult male skin and skull with dentaries from the Rawlinson Mountains, Huon Peninsula (6°43'S, 147°06'E), Papua New Guinea.

Diagnosis. Frontals and rostrum showing extreme inflation; dorsal grey tone with less frosting as white bands are less sharply expressed; little mid-dorsal darkening; white ventral

Fig.6. Distribution of *Mallomys aroaensis*. Star = type locality.

zone narrower than in *M. a. aroaensis;* tail has 8 or 9 scales per cm of length, on upper end of range for species.

Discussion. *Type specimen.* Although De Vis' description of *Dendrosminthus aroaensis* was somewhat unconventional (see introduction), it is nonetheless sufficient according to the Code of Zoological Nomenclature to allow the name to stand as valid. Soon after De Vis' description, the type specimen sank into obscurity. Longman (1916) reports that the skin had been lost, but that the skull remained. The identity of the skull, however may have been confused. Tate (1951:275) notes that only the front half of the skull was preserved, but on p.373 he gives a condylo-incisive length. In both places he notes the specimen number as "Queensland Museum No. 2814", but on p.275 he records it as male, and on p.373 as female. Although De Vis (1907) gives no specimen number, he does note that the type is a male. A search by one of us (K.A.) of the Queensland Museum collections revealed that only one *Mallomys* specimen is presently held in that institution. It is represented by a complete skull (QM J2814), which is listed in the register as the type of *M. aroaensis*. There is no mention of a skin, and at first no trace of the skin of the holotype could be found. However, a search of a drawer labelled "Foreign Mounts" revealed a study skin of a *Mallomys* specimen in poor condition, lacking the right pes and with brittle skin (see Figs 11-12). The skin is clearly male as it has a large epididymal sack. A wooden label attached to the specimen reads "*Dendrosminthus aroaensis* de Vis Aroa R. B N Guinea E28 Type". There can be no doubt that this specimen is the previously lost study skin of the holotype of *Dendrosminthus aroaensis*.

There is also no doubt that *M. aroaensis* constitutes the first valid name for the lower altitude grey-furred species of *Mallomys*. In all ways it is consistent in morphology with specimens referred to this taxon here, showing the characteristic inflated rostrum, round mesopterygoid fossa, grey dorsal (with an ill-defined dark dorsal stripe) and white ventral colouration.

Range. This species as presently interpreted is restricted to Papua New Guinea. Specimens of the subspecies *M. a. aroaensis* are recorded from Mount Sisa (190 km east of the Irian Jayan border) to Mount Simpson in far eastern Papua New Guinea. *Mallomys a. hercules* is restricted to the Huon Peninsula, and represents the only occurrence of *Mallomys* off the Central Cordillera. There they extend to 3,600 m in altitude. At some locations (e.g. Mount Sisa), *M. aroaensis* is far more common than other species, while throughout the eastern end of its range (from Mount Scratchley to Mount Simpson), it is the only *Mallomys* species to be found. It has been recorded from as low as 1,100 m on Mount Sisa, Southern Highlands Province (e.g. AM M16693), to 2,000 m on Mount Albert Edward (AM M12858), and 2,450 m at Baiyanka (BM 47.1339-40) and on Lamende Range, northwest of Mount Giluwe (BM 53.349-50). At this latter locality the species is sympatric with (or perhaps stratified just below) *M. istapantap* n.sp.

Variation. Because of the variability present in *M. r. weylandi,* the possibility needs to be discussed that *M. aroaensis* and *M. rothschildi* in Papua New Guinea represent a single, highly variable taxon. We have carefully considered this possibility, and feel that the overwhelming evidence indicates that the material includes two distinct species. Distinct and consistent differences in pelage, relative tail length, number of tail scales, and somewhat less constant differences in nasal length rostrum width and interorbital width all support the division into two taxa. The range of morphological and external variation present in this sample from Papua New Guinea is far greater than that seen in *M. r. weylandi* from Irian Jaya. Furthermore, the two groups behave as species in the field. They occupy different nesting sites, and some factor or factors, including competitive exclusion, often ensures that one or the other species is dominant at any one locality.

There is little doubt but that the Huon Peninsula *Mallomys* is correctly referred to *M. aroaensis,* of which it is however a distinctive subspecies. There remains one problem: whether all other Papua New Guinean populations are consubspecific. In general, skins here referred to nominotypical *M. aroaensis* are greyish, with grey bases to the hairs, followed by clear but not sharply marked alternating black and white bands, usually two pairs, the tips being white; long guard hairs, with blackish bases and long white tips, protrude through the coat of contour hairs. Younger specimens are more distinctly frosted; the white tips of the guard hairs wear down with age. The midback has always some degree of darkening, and the shoulders and thighs tend to be lighter. There is clearly expressed geographic variation in details of this pattern. Specimens from the Mount Simpson area, of the far south-eastern Papua New Guinea mainland, are rather uniform, light grey, with most prominent mid-dorsal darkening; those from the Aroa and Angabunga Rivers are rather more yellow tinged; and skins from more westerly localities are medium to dark grey. The ventral zone is creamy to yellow toned in the Mount Simpson skins, and this sort of tone is found as far west as the Hagen Range; west of Mount Hagen, however, the tone is more purely creamy. This variability makes it seem possible that future research will result in the subdivision of our taxon *M. a. aroaensis*.

Reproduction and nest sites. Reproduction and diet in the species are poorly known. Two of us (TF, KA) collected a female from a burrow near Kosipe, altitude 2,000 m, on Mount Albert Edward on 27 Dec. 1981. She was carrying a late term naked foetus with a head body length of c.80 mm, but it was lost to dogs before further measurements could be obtained. A second female pregnant with a single foetus was taken by K.A. on Mount Sisa on 14 Oct. 1985.

Substantial data suggests that this taxon usually nests in burrows. Two of the authors' (T.F., K.A.) personal experience in Central and Southern Highlands Province, and the testamony of many Papuan informants supports this. We know of no records of animals being found in tree hollows.

Mallomys istapantap n.sp.

Figs 1-2, 11-12, Tables 4-5

Type material. HOLOTYPE: AM M7328, female study skin and skull with dentaries collected at Korelum, Mount Hagen district

(5°52'S, 144°14'E) on 17 July 1945 by Captain Neptune B. Blood.

PARATYPES: AM M12908, female skull with dentaries and hand and foot in alcohol, collected on the margin of the Neon Basin, 2,900--3,000 m, Mount Albert Edward (8°28'S, 147°20'E) on 20 Dec. 1981 by K. Aplin; AM M12875, juvenile female, flat skin with skull and dentaries (young of M12908, locality as for M12908); CM 15611, male study skin and skull with dentaries and partial skeleton. Collected at Kilenbokingl 3,650 m, Mount Wilhelm (5°49'S, 144°57'E) on 30 July 1970 by J. Hope; CM 15612, female study skin and skull with partial skeleton. Data as for CM 15611; CM 15682, female study skin and skull with partial skeleton. Collected on Mount Wilhelm, on 14 Aug. 1969 by J. Hope; CM 15684, male study skin and skull with dentaries and partial skeleton. Collected at Lake Koromonk, 3,850 m (6°06'S 143°18'E) Mount Wilhelm on 6th Aug. 1969 by J. Hope; CM 15681, male study skin and skull with dentaries and partial skeleton. Collected at Mondia, Mount Wilhelm (2,900-3,000 m) on 3 Oct. 1969 by J. Hope.

Etymology. Pronounced "ee-stap-an-tap", from "I stap antap", a Melanesian pidgin term meaning literally "it is above", frequently used in conjunction with animals and plants found only on mountaintops. Thus, "*Mallomys* from the mountaintops".

Diagnosis. *Mallomys istapantap* n.sp. differs from all other *Mallomys* species in having paler ears, in the shape of the maxillary-premaxillary suture (Fig. 2), the greater extent of the alisphenoid contribution to the edge of the postglenoid vacuity (Fig. 2), the elongate and dorsoventrally flattened sphenopalatine foramen (Fig. 2), the elliptical shape of the mesopterygoid fossa (Fig. 2), and the gentle (rather than steep) way in which the posterior edge of the palate slopes towards the mesopterygoid fossa (Fig. 2). Its large size, hypsodont molars, excessively thickened palate, short tail and long thick underfur further distinguish it from all species except *M. gunung* n. sp. It has a very long depigmented zone on the tail (often some three quarters of the total length as in *M. rothschildi*) It differs from *M. aroaensis* in that there is no dorsal stripe, and the body contour hairs are unbanded, dark, but the plentiful thick underfur gives it an overall grey tone. Furthermore, more of the masseteric foramen is hidden behind the zygomatic plate when the skull is viewed from the side than in other species of *Mallomys* (Fig. 1), and the parietal crests are generally less well developed.

Description. *Skull.* The skull of the holotype is in good condition, but the left bulla is missing and the pterygoids are damaged. It is from a relatively young but clearly adult animal. The incisive foramina are slightly asymmetrical, the left one being longer than the right. The bony palate is greatly thickened, and its surface is ornamented by a median crest and two lateral crests that run close to the molar alveolar margin. These ridges coalesce at the posterior margin of the bony palate. Posteriorly, the palate slopes gently upwards and backwards to intersect the sloping ventral wall of the mesopterygoid fossa. These surfaces meet in the middle of the rear face of the bony palate. The nasals terminate abruptly posteriorly, there being almost no wedging into the frontals. The nasals maintain an even width for their posterior half, but widen rapidly anteriorly. The nasal tips do not overhang the premaxillae. The premaxillary/maxillary suture has the "S" shape

Fig.7. Distribution of *Mallomys istapantap* n.sp. (closed circles and star), and *M. gunung* n.sp.(open circles and star). Star = type locality.

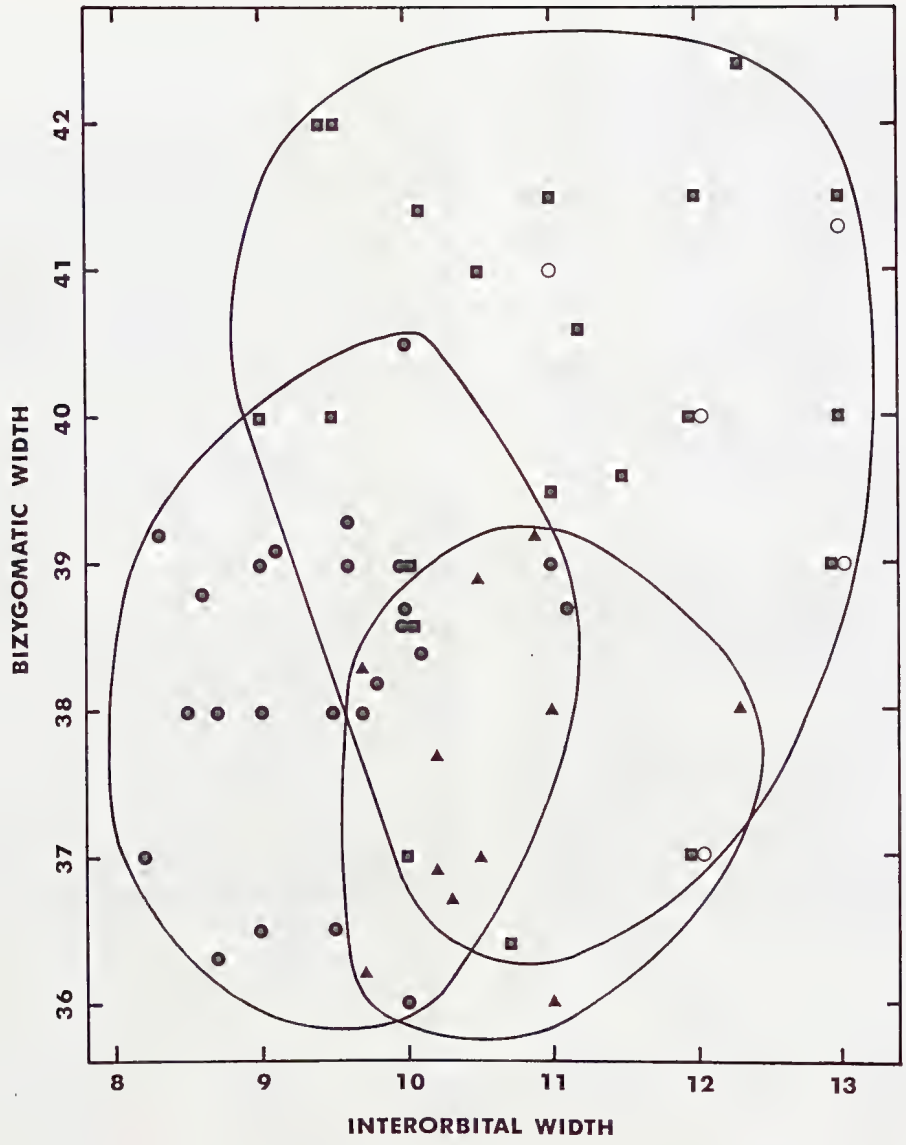

Fig.8. Bivariate plot of bizygomatic width over interorbital width for *Mallomys aroaensis aroaensis* (squares), *M. a. hercules* (open circles), *Mallomys rothschildi rothschildi* (solid dots) and *M. r. weylandi* (triangles).

characteristic of this species (Fig. 2). The premaxillae project posteriorly alongside the nasals, but terminate 3 mm anterior to the nasal/frontal suture. When viewed from above, the rostrum has a distinctly step-shaped form. Anteriorly, the lateral surfaces of the premaxillae are parallel sided until they approach the maxillary suture, when they expand rapidly. Just posterior to this suture, the lateral walls of the maxillae again assume a parallel orientation. The frontals are only slightly inflated, while the maxillary portion of the dorsal surface of the cranium is uninflated. The zygomatic plate is broad, and half to one third the length of the masseteric foramen is hidden behind it. The zygomatic arches are broad and sturdy, and the interorbital region is broad. Two poorly-defined supraorbital crests are present. Posteriorly, they diverge and weaken, to become very poorly-defined parietal crests. The mesopterygoid fossa is clearly elliptical with its long axis oriented dorsoventrally. The pterygoids are damaged therby obscuring much of their morphology. The bulla is as in other species of *Mallomys*.

The incisor morphology is as in other species of *Mallomys* The incisor enamel is pigmented orange, and is a deeper hue on the uppers than the lowers. The molars are very large and only lightly worn. The right M1/ has a small aberrant cuspule positioned just anteromedial to T2. Both M2/s have small T3's developed, a feature that we have not seen in other individuals of a species of *Mallomys*. The molars are also extremely high crowned. This is difficult to quantify as the molars wear rapidly, and even when lightly worn part of the crown base is still hidden in the alveoli. However, the height of the anterior of the crown of the M/1 of the holotype is c.5 mm. Apart from these differences, the crown patterns of the molars do not differ from those of other species of *Mallomys*. The dentary is similar to that of

other *Mallomys*.

Skin. The study skin of the holotype is in good condition. The mammae number is 1 + 2 = 6, and the nipples are small, possibly indicating that the animal was nulliparous. The dorsal surface is covered with dense, dark grey fur. The underfur of the midback is c.23 mm long, but numerous contour hairs project up to 10 mm beyond this, and the guard hairs extend a further 25-30 mm. The contour hairs are dark brown to black; because of the thickness of the underfur they make little contribution to the overall dorsal colour. Over most of the back the guard hairs have a short white tip (8-10 mm long). Over the shoulders and head, however, the white tips are very short or absent. The base of the underfur is dark grey, but has pale and dark tipping. The overall dorsal colouration is difficult to quantify owing to the intermixing of white, grey, brownish and black elements. It falls close, however, to Clove Brown or Blackish Slate. This colour persists onto the dorsal surface of the forelimbs. On the rump and dorsal surface of the hindlimbs, however, the colour is paler, being close to Slate Grey. There is an abrupt colour change to the ventral surface where the dark fur gives way to pure white with no guard hairs intermixed. Along the midline of the venter there are some hairs with an orange/yellow discolouration. This may be an artefact as the hairs are concentrated along the slit made into the body cavity, probably during preparation. Anterior to the forelimbs, the pure white of the venter gives way to short, grey underfur. This extends to within 10-15 mm of the lower lip, where very short brownish hairs are present.

The ears, hands and feet are clothed in short brown hairs on their dorsal surfaces. The flesh of the ears is pale, there is no dark eye ring, and the vibrissae are black. The pads of the hand and hindfoot are as in other species of *Mallomys*. The proximalmost 125 mm of the tail is dark, close to black. The distalmost 155 mm is white (in other specimens there is generally a much higher proportion of white). There are three hairs per tail scale, and 8 to 9 scales per cm in the middle of the tail. Most scales are rectangular, and approximately twice as broad as long.

Discussion. *Range*. *Mallomys istapantap* n.sp. is morphologically and electrophoretically (though *M. gunung* n.sp. is unknown in this latter respect) the most distinctive of the *Mallomys* species. Its large hypsodont molars and associated cranial adaptations make it easily recognisable, even as a partial trophy skull or skeletal pick up.

The distribution of *M. istapantap* n.sp. is intriguing. It appears to be restricted to subalpine herbfields and grassland, and bordering upper montane forest along the east-central portion of the New Guinean Central Cordillera. Within this area it seems to favour the upper montane forest/alpine grassland ecotone. Geoff Hope (personal communication) has commented that many of the C.M. specimens reported upon here come from this habitat, and we (T.F., K.A.) have

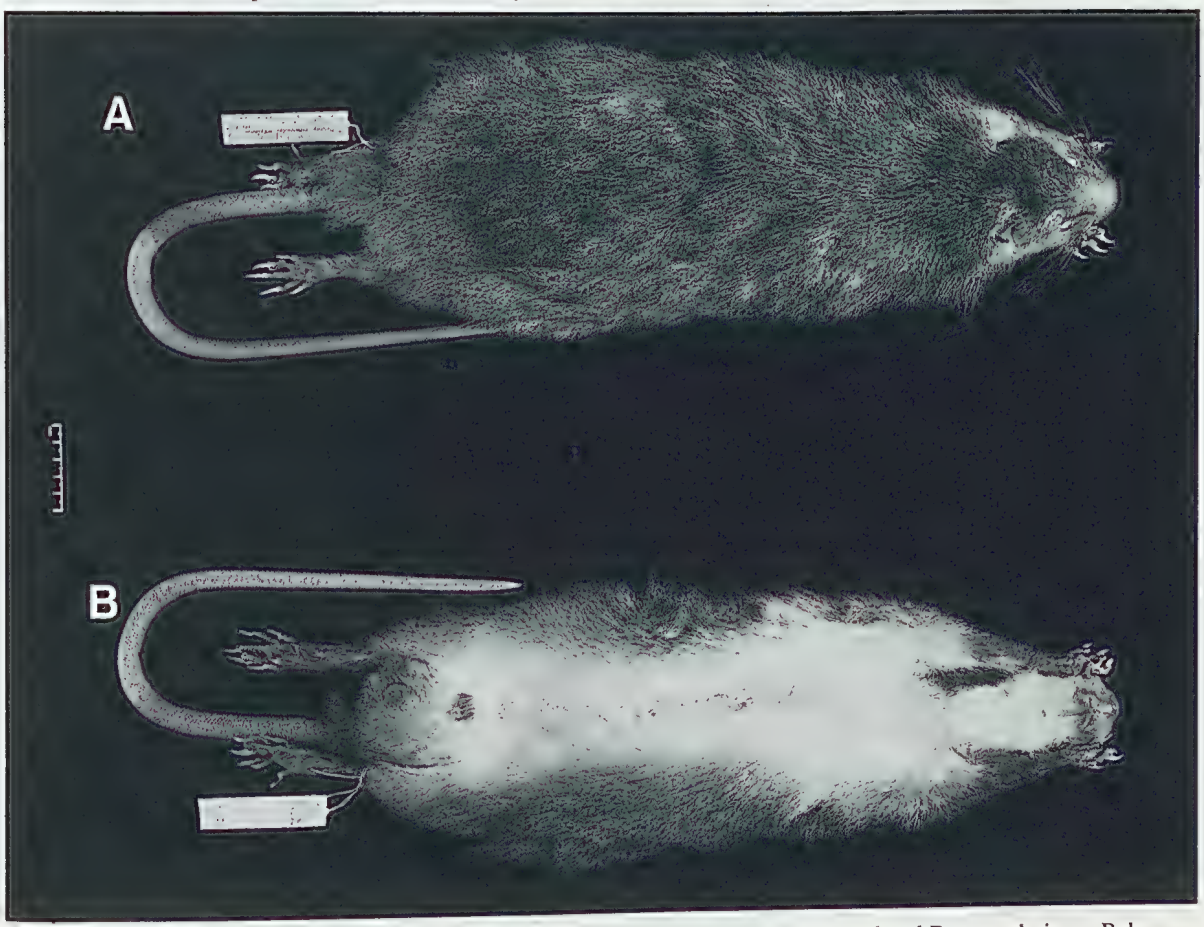

Fig.9. Skin of AMNH151336, *Mallomys rothschildi weylandi* (light phase) in A, dorsal and B, ventral views. Bele River, Irian Jaya.

also obtained specimens in this area. Altitude varies from "8,000 to 9,000 feet" (= 2,540 to 2,750 m) (BM 53.344 to 53.346 and 53.348) and "9,000 feet" (= 2,750 m) (BM 53.343 to 53.347 and 53.349) and 2,900 to 3,000 m (e.g. AM M12908, CM 15681) to 3,850 m (CM 15684) but the species may occur higher. The westernmost records for the taxon are from Mount Giluwe (Southern Highlands Province) but based on continuous high topography it seems likely that it occurs at least as far west as the Yuma Range to the east of Lake Kopiago. In the east, it is found as far as Mount Victoria (there is a partial pick up skull, AM M8209, from this locality) in the Owen Stanley Ranges. Its distribution in this region is doubtless disjunct, being limited to the higher peaks. It is fairly certain that this taxon is absent from the high ranges to west of the Strickland River in Irian Jaya. This is because moderate-sized collections of *Mallomys* skulls, which do not contain *M. istapantap* n.sp., are known from the Snow Mountains, Irian Jaya, where it seems to be replaced by *M. gunung* n.sp. On Mount Giluwe *M. istapantap* n.sp. in sympatric with *M. r. rothschildi*, while on the Lamende Range north-east of Mount Giluwe a specimen of *M. aroaensis* (BM 53.349) was collected at 2,450 m at the same time as some *M. istapantap* n.sp. at 2,540 to 2,750 m. However, it is unclear whether these two species exist sympatrically, or replace each other altitudinally in this area, as the altitude is near the known limit for both taxa.

Diet, reproduction and nest sites. Diet and reproduction in *M. istapantap* n.sp. are poorly known. The only data regarding reproduction known is that two of us (T.F., K.A.) collected a female (AM M12908) and a fully-furred young (AM M12875) from a burrow in a moss mound at 2,900 to 3,000 m on Mount Albert Edward on 20 Dec. 1981.

Biology. The large, hypsodont molars of *Mallomys istapantap* n.sp. suggest that it must cope with an abrasive vegetable diet. The teeth of other *Mallomys* species from high altitude areas sometimes suffer extreme wear (e.g. CM 11716), so high molar crowns may significantly increase the reproductive lifespan of an individual. Many alpine herbfields in montane New Guinea contain little grass, but hard and presumably abrasive ferns are common. These and other abrasive leaves may form a significant part of the diet of *M. istapantap* n.sp. Equally interesting from a dietary point of view is the degree of orange (iron) pigmentation in the incisor enamel. As noted previously, specimens of *M. rothschildi* and *M. gunung* n.sp. from high altitudes possess white incisor enamel, while those from lower altitudes have the normal orange colouration. However, even the highest altitude *M. istapantap* n.sp. that we have examined have orange incisor enamel. The widespread occurrence of species with pale incisor enamel in upper montane habitats (e.g. *Rattus richardsoni, Melomys albidens, Melomys fellowsi*) suggests that the ability to fix iron into the enamel matrix of the incisors may be affected by altitude. If this ability is greater in *M. istapantap* n.sp.

Fig.10. Skin of AMNH151352, *Mallomys rothschildi weylandi* (dark phase) in A, dorsal and B, ventral views. Bele River, Irian Jaya.

than *M. rothschildi* and *M. gunung* n.sp. this may well be a further adaptation to high-altitude living.

Mallomys gunung n.sp.

Figs 1-2, 11-12, Tables 4-5

Type material. HOLOTYPE: AMNH 151346, adult male study skin and skull with dentaries, collected at 3,800 m, 2 km east of Mount Wilhelmina (4°15'S, 138°45'E), Irian Jaya, Indonesia on 19 Sept. 1938 during the 3rd Archbold Expedition.

PARATYPES: AMNH 151437, adult male study skin and skull with dentaries collected at 3,650 m, 7km north-east of Wilhelmina Top (4°15'S, 138°45'E), Irian Jaya, Indonesia on 11 Sept. 1938 during the 3rd Archbold Expedition; AM M19029, sex unknown, anterior half of skull and dentaries only collected at 3,760 m, Moraine Camp, Meren Valley, Mount Carstenz (4°05'S, 137°11'E) on 9 Dec. 1983 by R.G. Peters; AM M19028, sex unknown, anterior part of skull only collected at 3,780 m, Moraine Camp, Mount Carstenz (4°05'S, 137°11'E) on 9 Dec. 1983 by R.G. Peters; AM M19030, sex unknown anterior part of skull collected at 3,500 m, Ertzberg Meadow, Mount Carstenz (4°05'S, 137°11'E) on 9 Dec. 1983 by R.G. Peters; CM 11716, sex unknown, partial skeleton with skull and dentaries collected at 4,050 m on Mount Carstenz (4°05'S, 137°11'E) by G.S. Hope.

Etymology. *Gunung* is Bahasa Indonesia for mountain, signifying its montane and Irian Jayan distribution. The name is thereby intended as an Indonesian equivalent of the Papua New Guinean *istapantap*.

Diagnosis. This species differs from all other *Mallomys* species in the retraction of the premaxillaries and nasals (Figs 2-3), a difference reflected in the short distance between the premaxillary/maxillary and nasal/premaxillary sutures, as well as the very short nasals relative to molar size (Table 5). It is also unique in the genus in its long, slender claws. It further differs from *M. aroaensis* and *M. rothschildi* in its larger molars, extensive palatal thickening, relatively shorter tail and lack of a dorsal stripe, and in the abundant, thick underfur. It differs from *M. istapantap* n.sp. in the shape of the premaxillary/maxillary suture, posterior bony palate morphology (both of which are as in *M. aroaensis*) and in having a round rather than sharply

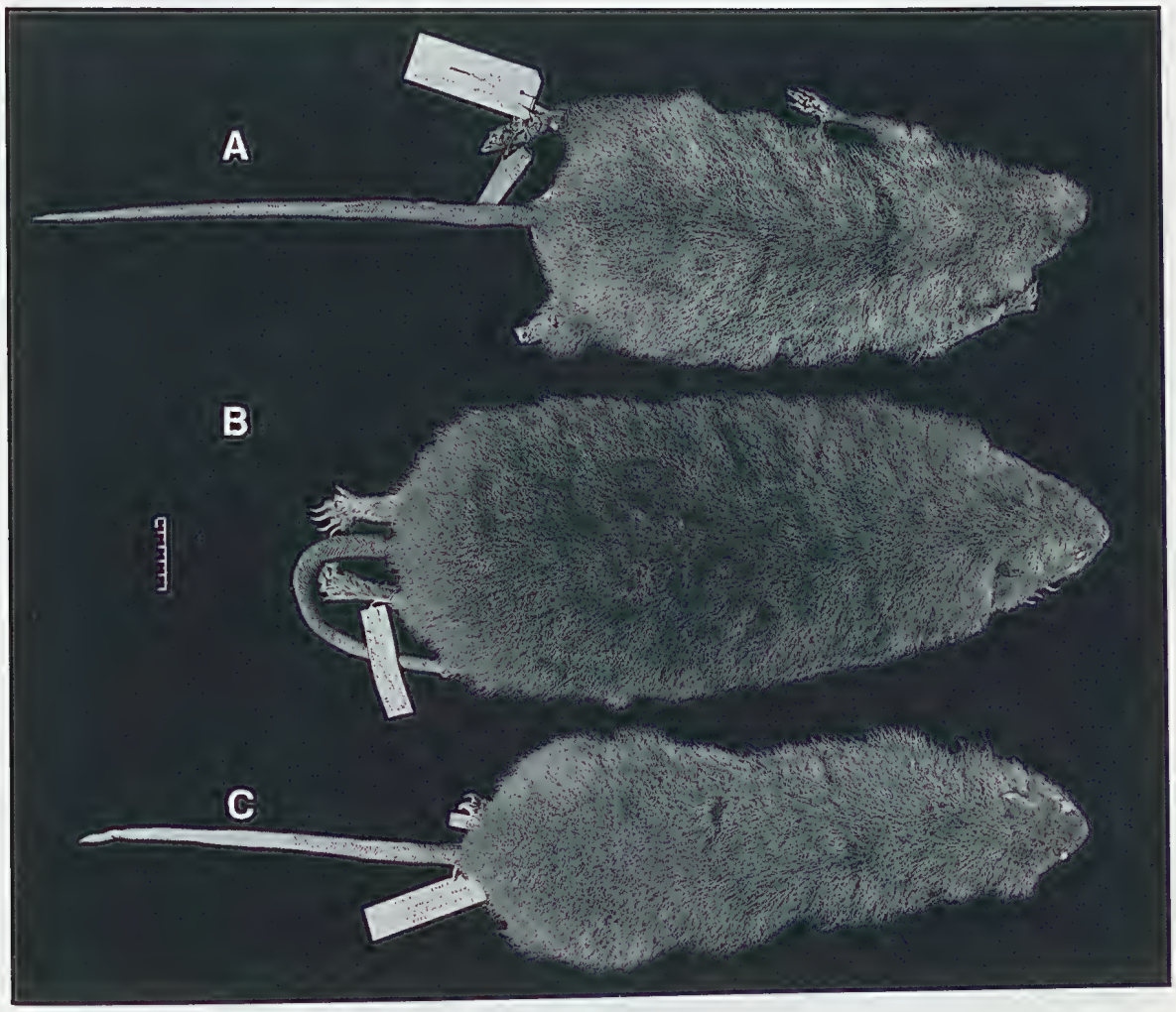

Fig.11. Dorsal views of study skins of the holotypes of A, QM J2814, *Mallomys aroaensis* (holotype); B, AMNH151346, *Mallomys gunung* n.sp. (holotype); and C, AM M7328, *Mallomys istapantap* n.sp. (holotype).

elliptical mesopterygoid fossa, and a pale (yellowish white) incisor enamel. Furthermore, the ears are darker than in *M. istapantap* n.sp, and the dorsum has more greyish rather than slightly brownish tones; the tail scales are more numerous (at least 9 per cm of length), but the depigmented zone is much shorter, only two thirds of the tail length at the most.

Description. *Skull.* The skull of the holotype is in good condition although the left zygomatic arch has been broken then glued back into place, and the left pterygoid is broken. It is from an adult with well worn molars. As in other species of *Mallomys,* especially *M. istapantap* n.sp., the bony palate is greatly thickened, with its surface ornamented by a sharp median crest. The posterior face of the bony palate slopes sharply to meet the gently sloping ventral floor of the mesopterygoid fossa. The incisor enamel is very pale yellow. The part of the premaxillae supporting the incisors projects markedly anteriorly, such that when viewed from the dorsal aspect, the incisors can be seen projecting well clear of the nasals. The dorsal part of the premaxillae and the nasals are short relative to other *Mallomys* species. The maxillary/premaxillary suture is almost vertically oriented. The rostrum is narrow as in *M. rothschildi,* and the interorbital region is very deeply dished. The sphenopalatine foramen is large, oval shaped and clearly visible as in *M. rothschildi.* The interparietal is divided into left and right parts by a suture in two of the three available crania. This is a rare feature otherwise in the genus. The interparietal is squarer than in *M. rothschildi.* The zygomatic arches flare broadly, and the parietal crests are well developed and subparallel. They are best developed anteriorly, becoming poorly defined in the region of the interparietal. The masopterygoid foramen is round and the bulla as in other species of *Mallomys.* The basisphenoid possesses a sharp medial ridge.

The incisors, although similar in morphology to those of other species of *Mallomys,* are much paler in colour than all except some high altitude *M. rothschildi* from Papua New Guinea. The uppers and lowers are similarly coloured, being a pale yellow. The molars are very large and hypsodont, closely resembling those of *M. istapantap* n.sp. in morphology. The dentary is as in other *Mallomys.*

The study skin of the holotype is in good condition. The dorsal surface is clothed in dense, grey fur, slightly lighter than and lacking the brownish tinge of *M. istapantap* n.sp.; blackish contour hairs protrude through it. The guard hairs

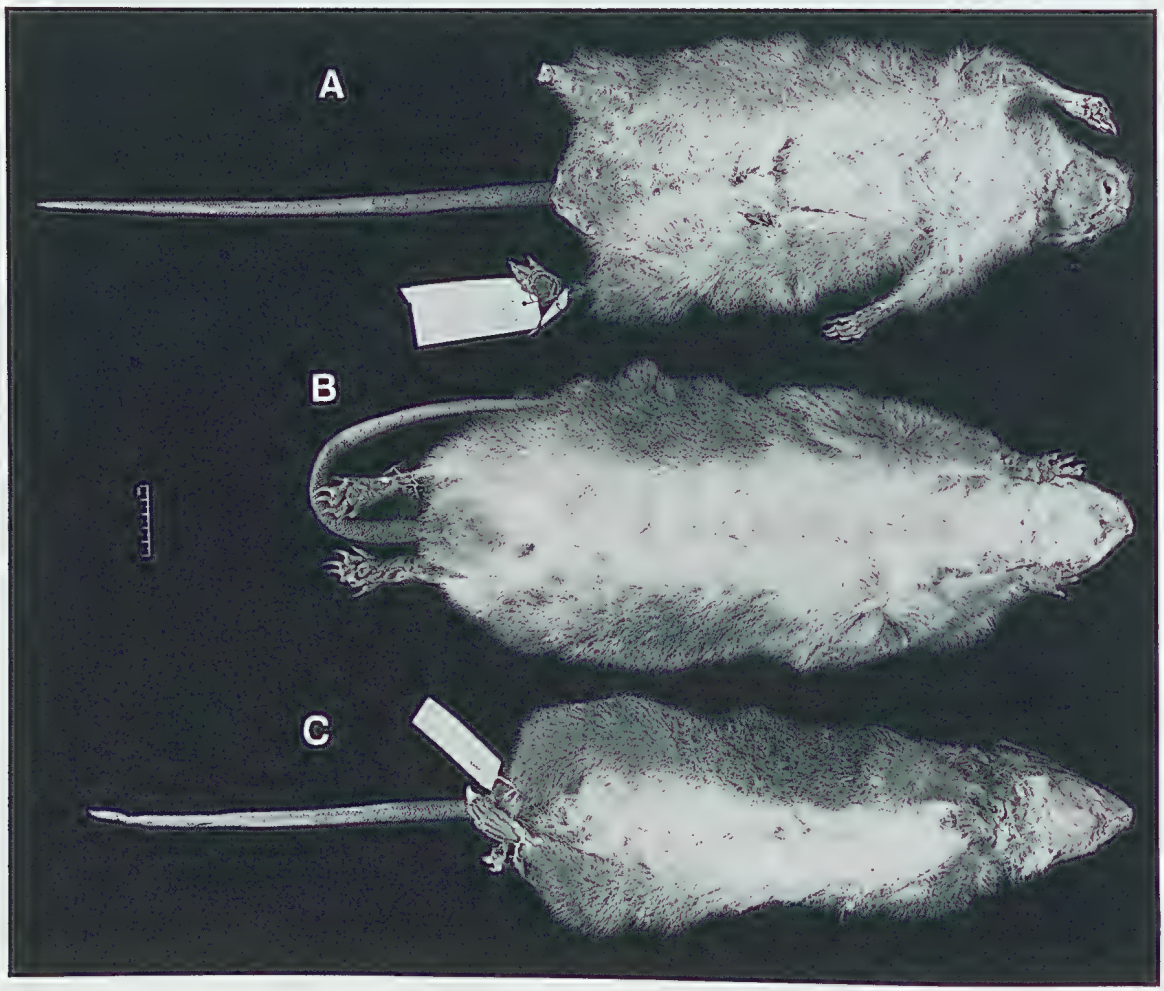

Fig.12. Ventral views of study skins of the holotypes of A, QM J2814, *Mallomys aroaensis* (holotype); B, AMNH151346, *Mallomys gunung* n.sp. (holotype); and C, AM M7328, *Mallomys istapantap* n.sp. (holotype).

all possess long (about 20 mm) white tips. The underfur is approximately 35 mm deep on the back, with the guard hairs extending a further 35 mm beyond that. As in *M. istapantap* n.sp. the guard hairs of the shoulders and head lack white tips. The ventral surface is covered in long, yellowish white fur, with no dark guard hairs intermixed. This pale fur extends anteriorly to the lower lip.

The ears are blackish and have a very fine covering of dark hairs. The hands and feet are clothed in long, coarse mixed dark and light hairs, with pale hairs predominating on the digits. The claws are unusually long and gracile, differing markedly from the more robust, shorter claws of other *Mallomys* species. A distinct dark eye ring is present and the vibrissae are black. The proximal most 125 mm of the tail is black, the distal portion (190 mm) being yellowish. There are three hairs per tail scale, and nine scales per cm in the middle of the tail. Most scales are roughly rectangular, and approximately twice as broad as long.

Discussion. *Range.* The cranial morphology of *Mallomys gunung* n.sp. is so distinctive that the species can be recognised quite easily on the basis of cranial fragments such as are often found as pick ups or in archaeological sites. Indeed, the majority of records of this taxon at present are from such material. Hope (1976) reported upon archaeological material that she assigned to *Mallomys rothschildi* from Mapala rockshelter, located at 3,996 m on Mount Carstenz. These specimens (AM F54828 and F54829) clearly represent *M. gunung* n.sp. The AM and CM paratypes of this species are all pick ups, found in the alpine meadows of the Carstenz area. The only specimens collected as whole animals thus far known are the holotype, collected 2 km east of Mount Wilhelmina, and the AMNH paratype, collected 7 km north-east of Mount Wilhelmina. This limited information indicates that *M. gunung* n.sp. has a restricted distribution centred on the alpine meadows of the Snow Mountains. The lowest elevations recorded are 3,500 m at Ertzberg Meadow, and the highest 4,050 m. However, the species may extend to higher elevations, as Hope (1976) notes "...There seems to be no doubt that on Mount Jaya this species [most probably *M.gunung* n.sp.] inhabits not only the grassland of the Kembau Plateau, but the most barren and inhospitable areas of the mountain as well..." (Hope, 1976:218). Nothing is known of the life history of this species.

Discussion

Phylogenetic relationships. Because we can identify no close outgroup for the species of *Mallomys*, and because of the nature of character distribution within the genus, it is difficult to interpret relationships at present. *Mallomys istapantap* n.sp. and *M. gunung* n.sp. share a number of similarities; it is unclear in most cases if the condition exhibited by these taxa is plesiomorphic or derived. The lack of a dorsal stripe, short tail, large molars and overall large size are of uncertain polarity, although we think they are probably derived; the hypsodont condition of the molars seen in both of these taxa is clearly highly derived, but may well be due to convergence, as both species are restricted to a similar environment (alpine meadows) and thus may have similar diets. These similarities aside, we can find no compelling evidence to suggest that they are close relatives. Both species possess a number of unique morphological adaptations within the genus. In *Mallomys istapantap* n.sp. these are centered in the bony palate, mesopterygoid fossa and rostrum whereas *Mallomys gunung* n.sp. has unique incisors and rostral morphology. The electrophoretic distinctiveness of *M. istapantap* n.sp. is suggestive of an early derivation within the evolution of the genus. However, because *M. gunung* n.sp. is unknown electrophoretically, this does not help in determining the relationship between the two high altitude taxa.

Considerable evidence suggests that the two lower altitude species, *Mallomys rothschildi* and *M. aroaensis*, are close relatives. They are closer to each other electrophoretically than either is to *M. istapantap* n.sp. and furthermore display a great degree of phenetic similarity. Unfortunately, due in part to lack of a suitable outgroup, we have been unable to identify any synapomorphies uniting these two species. The principle of metachromism (Hershkovitz, 1968) indicates that the agouti-banded hair type of *M. aroaensis* is more primitive than the saturated black of *M. rothschildi;* but the inflated rostrum and frontals of the former are presumably the more derived condition. Thus neither can be regarded as wholly primitive. It can be noted that the two high altitude species both have saturated-patterned contour hairs, so presumably relate in this respect to *M. rothschildi.*

Zoogeography. The distribution of the species of *Mallomys* poses some interesting questions. With the exception of *M. aroaensis,* which occurs on the Huon Peninsula, all *Mallomys* are restricted in distribution to the New Guinean Central Cordillera. *Mallomys rothschildi* is a widespread species, being present from the Weyland Range in the west to the Aroa River in the east. Interestingly, the Huon Peninsula form, *M. a. hercules,* resembles *M. rothschildi* to some degree. This latter species is absent from the high Huon Peninsula. *Mallomys istapantap* n.sp. and *M. gunung* n.sp. have the most restricted range, probably occupying disjunct alpine and subalpine habitats only.

The degree of sympatry between the species of *Mallomys* is difficult to establish. It is evident that in some areas where extensive sampling has been undertaken, only a single species is present; examples include the presence of only *M. aroaensis* on the Huon Peninsula and in the far southeast, as already pointed out, and of *Mallomys gunung* n.sp. high in the Snow Mountains. In other locations we have specimen-backed evidence for two species sympatry: *M. rothschildi* and *M. aroaensis* on Mount Elimbari and the Schrader Range, and *M. rothschildi* and *M. istapantap* n.sp. on Mount Giluwe. Furthermore, collections in the Australian Museum show that three species (*M. istapantap* n.sp., *M. rothschildi, M. aroaensis*) exist in close proximity if not in sympatry in the Mount Hagen area. At some well documented locations, one species seems to predominate, with a second being much rarer (e.g. *M. rothschildi* at

Telefomin, Baiyanka, Yanka, and Mount Elimbari; and *M. aroaensis* at Mount Sisa). Such patterns of distribution may become more easily understood when more is known about the ecology of these taxa.

Many upper montane species are spread throughout the Central Cordillera (e.g. *Phalanger sericeus, Pogonomelomys ruemmleri*). Although populations of these taxa may be disjunct today, it is probable that continuous suitable habitat (and thus populations) were found along the entire Central Cordillera during Pleistocene glacial maxima. The fact that some species were clearly able to occupy all of this range, while others were unable to spread, may be related to precise habitat needs. In the instance of the *Mallomys* species it seems possible that *M. istapantap* n.sp. and *M. gunung* n.sp. are more strictly tied to subalpine grassland than the other mammalian taxa that occur within and around this vegetation type. Tracts of upper montane forest thus may have acted as a barrier to these giant rats, but not less ecologically restricted species.

Summary

Electrophoretic and morphological evidence concur as to the presence of three species of the genus *Mallomys* in Papua New Guinea. Additional morphological analysis indicates the presence of a fourth species, in the high mountains of central Irian Jaya. Examination of all type material indicates that only two of the four species are previously named. The correct names for these taxa are *Mallomys rothschildi* Thomas, 1895 and *Mallomys aroaensis* (De Vis, 1907). The remaining species are described as new: *Mallomys gunung* n.sp. and *Mallomys istapantap* n.sp. Two distinct subspecies of *M. rothschildi, M. r. weylandi* (western New Guinea), and *M. r. rothschildi* (eastern New Guinea) can be recognised. Two subspecies of *M. aroaensis, M. a. aroaensis* (from the Central Cordillera in Papua New Guinea) and *M. a. hercules* (from the Huon Peninsula) can also be discerned. *Mallomys gunung* n.sp. is restricted to subalpine and alpine habitats in the Snow Mountains, while *M. istapantap* n.sp. is restricted to subalpine grassland and upper montane forest in the eastern and central parts of the Central Cordillera. The three Papua New Guinean species may exist in sympatry in parts of eastern New Guinea.

ACKNOWLEDGEMENTS. We owe a great debt of thanks to the staff of the Evolutionary Biology Unit of the South Australian Museum for analysis of the electrophoretic material that is presented here. Others who have assisted greatly with this project include all of the staff of the Division of Wildlife, Papua New Guinea, particularly Mr Lester Seri. Furthermore, Mr Karol Kisokau, Secretary of the Department of Environment and Conservation, deserves special thanks for the invaluable help that he extended to Flannery and Aplin during their stays in Port Moresby. Special thanks must also go to Dr Guy Musser of the American Museum of Natural History, for his loan us specimens and his constructive criticisms of an earlier draft of this paper; and to Dr John Calaby of CSIRO Wildlife Research for loans of specimens.

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Ms Barbara Duckworth composited the plates for this paper and drew the figures. Ms Kate Lowe took the photographs. Ms Tina Goh typed the manuscript.

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Accepted 23 September 1988

APPENDIX I

Enzymes and proteins examined during electrophoresis: Aconitate hydratase (ACON, E.C. 4.2.1.3), acid phosphatase (ACP, E.C. 3.1.3.2), adenosine deaminase (ADA, E.C. 3.5.4.4), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), adenylate kinase (AK, E.C. 2.7.4.3), carbonate dehydratase (CA, E.C. 4.2.1.1), diaphorase (DIA, E.C. 1.8.1.4), enolase (ENOL, E.C. 4.2.1.11), fructose-diphosphatase (FDPASE, E.C. 3.1.3.11), glyceraldehyde-phosphate dehydrogenase (GAPD, E.C. 1.2.1.12), aspartate aminotransferase (GOT, E.C. 2.6.1.1), glucose-6-phosphate dehydrogenase (G6PD, E.C. 1.1.1.49), glycerol-3-phosphate dehydrogenase (GPD, E.C. 1.1.1.8), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), leucine aminopeptidase (LAP, E.C. 3.4.11.1), lactate dehydrogenase (LDH, E.C. 1.1.1.27), malate dehydrogenase (MDH, E.C. 1.1.1.37), mannose-phosphate isomerase (MPI, E.C. 5.3.1.8), purine nucleoside phosphorylase (NP, E.C. 2.4.2.1), peptidases (PEP, E.C. 3.4.11? or 13.4.13?), 6-phosphogluconate dehydrogenase (6PGD, E.C. 1.1.1.44), phosphoglycerate kinase (PGK, E.C. 2.7.2.3), phosphoglucomutase (PGM, E.C. 5.2.4.2.), pyruvate kinase (PK, E.C. 2.7.1.40), superoxide dismutase (SOD, E.C. 1.15.1.1), and L-iditol dehydrogenase (SORDH, E.C. 1.1.1.14).

APPENDIX II

Specimens Examined (excluding types)

Mallomys r. rothschildi CM3958 Mount Giluwe; CM16518, 15683, 12687 Mount Wilhelm; AM M15603, AM M15745-15748, M15625-15626, M15627, M15628, Mount Elimbari; AM M9083 Schrader Range, AM M6930 Mount Hagen area; AM M9534 Tomba, Hagen Range; AM M13730, AM M17361-17362, AM M15999 Telefomin; BM69-338 Schrader Range; BM53.340-2 Hagen-Giluwe area; BM53.345, Mount Giluwe; BM50.1784-7,9,90,92 Hagen Range; BM50.1780 Mount Wilhelm, BM47.1334-8 Bismarck Range; BM 39.3974 between Mounts Musgrave and Scratchley (type of *M. rothschildi*).

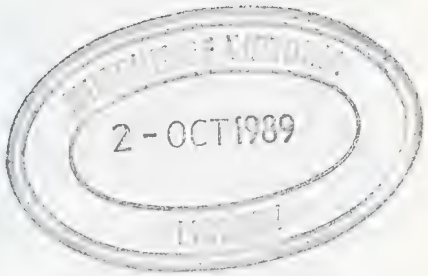
Mallomys r. weylandi AMNH103261, 101949 Weyland Range, AMNH151333-151334, 6, 8-40, 51-2, Bele River-Mount Wilhelmina area, Irian Jaya.

Mallomys a. aroaensis AM M6931 Hagen area; AM M16693, 15629-15630, 17096, 17893-17894 Mount Sisa, Southern Highlands; M9583 north slopes Wahgi Divide, Jimi Valley; AM M8590 Wonenara, eastern highlands; BM47.1242-3 Ramu River; BM50.1191 Kratke Mountains.; BM50.1781 Mount Wilhelm; BM47.1339 Purari-Ramu Divide; BM53.363-7 Mount Giluwe; BM53.337-9 BM50.1783,8, 91-7, Hagen Range; BM50.1193-8 Bubu River district; BM1939.1945, Aroa River; BM1939-1944 Angabunga River; BM47.1341,44-55, Mount Simpson.

Mallomys a. hercules RMNH 29251, 292 Huon Gulf; RMNH 29292, 230 Rawlinson Mountains.

Mallomys istapantap n.sp. AM M8209 Mount Victoria; RMNH10446 north of Lake Aunde, Mount Wilhelm; AMNH192178 Mount Otto (near summit). BM 53.343,-4,-6,-7,and -8 Mount Giluwe". BM 53.349 Lamende Range, north-west of Mount Giluwe. CM16730-1 Lake Bendenumbum Mount Giluwe, CM15688 Mount Giluwe.

Mallomys gunung n.sp. AM F54828-9 Mapala rockshelter, Mount Carstenz, Irian Jaya.



Scolodera pardalotus n.gen., n.sp. (Mantodea, Mantidae) from Northern Queensland, Australia

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Abstract. A new mantid genus and species, *Scolodera pardalotus*, is described from the Mareeba district in north-eastern Australia.

Milledge, G.A., 1989. *Scolodera pardalotus* n.gen., n.sp. (Mantodea, Mantidae) from northern Queensland, Australia. Records of the Australian Museum 41(2): 107-110.

The mantodean fauna of Australia is quite distinctive, although rather impoverished (Beier, 1968). For example, in the Mantinae, nine of the 14 genera recorded from Australia are endemic or also occur in New Guinea (Balderson, 1984). The genus described here apparently has no close associations within either this group or the more widespread Asian element. Its possible relationships are discussed in this paper.

The terminology used in describing the genitalia follows La Greca (1953-1954). For examination purposes the genitalia were prepared by relaxing the specimen for 48 hours, then dissecting out the genital complex and immersing it in 10% KOH for 24 hours at room temperature. It was then washed and transferred to 70% alchohol, and the soft internal tissues were teased out. The genital complex is stored in glycerol in a small vial attached to the specimen pin.

The holotype is lodged in Australian Museum, Sydney. It is the only specimen of this new species known at present.

Scolodera n.gen.

Type species. *Scolodera pardalotus* n.sp.

Diagnosis. Male only, female unknown. Of medium stature. Head triangular from anterior aspect, wider than high, shallowly concave anteriorly; eyes prominent, margins rounded; facial shield transverse with narrow transverse ridge near upper margin curving dorsally between antennae, each lateral margin with a bulge which projects ventrally.

Prothorax moderately elongate; prozona dorsally somewhat swollen in anterior half, posterior half with low diagonal ridge on each side of midline, ventrally with large spiniform process on each side anterior to coxal insertion; dorsal surface of metazona anteriorly with 2 large spiniform projections side by side and directed dorsolaterally, bulging slightly at posterior margin on either side of midline, without distinct median carina.

Outerface of forecoxa with distinct median ridge.

Forefemur with 3 discoidal spines, 1st and 3rd short, 2nd much longer; with 4 outer spines, the first 3 rather long, and 13 inner spines; claw groove centrally situated. Foretibia with 6 outer and 12 inner spines. Mid and hind legs moderately long.

Tegmina and wings elongate, surpassing tip of abdomen; abdomen narrow and elongate; cerci of moderate length, cylindrical. Genitalia with distal process undivided, medial arm partially sclerotized, anterior apodeme elongate narrow to the right and broadly squamiform to the left, ventral sclerified process small and U-shaped, ventral plate fused to main body of phallomere.

Etymology. The generic name is derived from the Greek *skolos* meaning thorn and *dere* meaning neck. The gender is feminine.

Scolodera pardalotus n.sp.

Figs 1-6

Type material. HOLOTYPE, male, Lock Creek, Davies Creek Road, Lamb Range, Mareeba district, North Queensland, 25 Dec. 1976, M.S. & B.J. Moulds. (Dry specimen. Australian Museum, Sydney).

Diagnosis (male). Colour of dry specimen pale yellow-brown, peppered with blotches and spots of blackish brown (Fig. 1). Head capsule (Fig. 2) with narrow black band on each side anteriorly, extending from middle of eye margin down beside facial shield onto inner margin of mandibles; a broader dark band on each side extending somewhat diagonally from upper inner margin of eye and fading dorsally toward neck; also with a central black band extending from neck to base of central ocellus; facial shield with thin central blackish stripe and a broader pale brown stripe on each side before marginal bulge; posterior part of head black with pale spot on external half of each side; antennae pale yellow brown, slightly more than twice the length of prothorax.

Prothorax (Fig. 3) with margins distinctly lamellate, especially at supracoxal expansion and with scattered, very small, tubercles; dorsal surface pale yellow-brown with large black blotches; prozona dorsally with a few scattered tubercles anteriorly and a few smaller ones posteriorly, slightly depressed centrally, ventrally dark brown with black blotches; metazona with a few small scattered tubercles dorsally, smooth and pale ventrally except for small dark area at base.

Forecoxa (Fig. 4) with outerface pale and darkly blotched; anterior margin with 7 elongate, blunt tipped spines; innerface pale with black band at proximal and distal ends. Forefemur with 1st and 3rd discoidal spines pale, 2nd black on innerface; 1st outer spine pale, rest black; long inner spines black, short ones pale; innerface of femur pale with large blackish patch just anterior to claw groove and a smaller one at grooming brush. Foretibial spines all tipped blackish. Mid and hind femur with distinct genicular spine.

Tegmen with costal margin opaque creamish above, brighter yellow ventrally toward base, major veins blackish; remainder of tegmen hyaline except for a number of the cross veins flushed blackish and a blackish patch at either end of the stigma. Wing with veins pale yellowish, especially in costal area, a few small cross veins near tip flushed brown, remainder of wing hyaline.

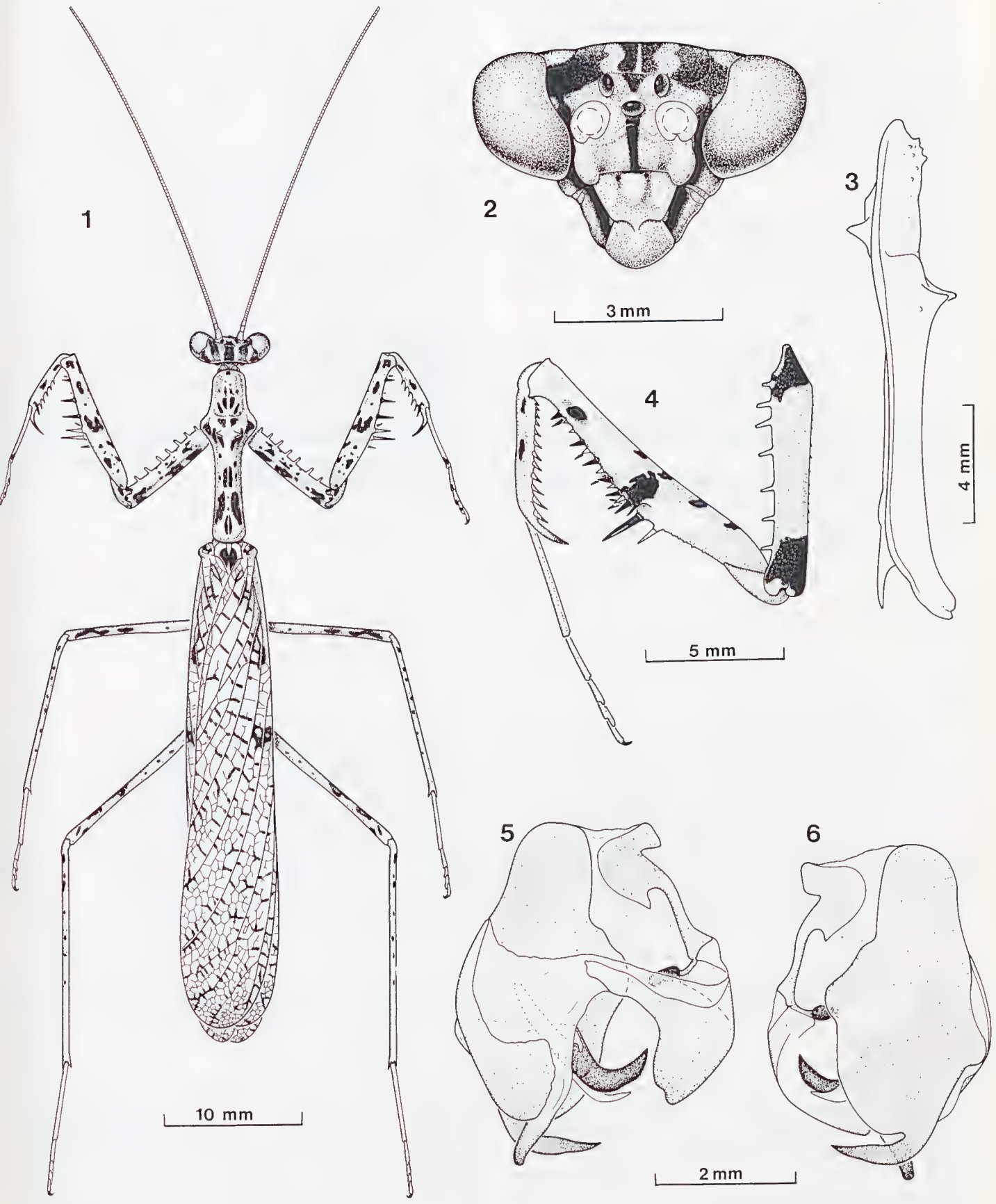
Abdomen brownish, cerci with apical segments somewhat beaded in appearance. Genitalia (Figs 5,6) with distal process elongate spiniform, sharply curved at base and directed dorsolaterally; apical process curving dorsally and blunt tipped; phalloid apophysis a stout uncinate spine, lightly shagreened, with a curved groove near base, anterior process narrow elongate; anterior portion of ventral lamina of left dorsal phallomere roughly triangular in shape with elongate process at junction with phalloid apophysis; main lobe of right dorsal phallomere with notch near apex.

Measurements. Total length 53 mm. Head width 6 mm. Head depth 4.5 mm. Pronotal length 13.3 mm. Pronotal width 4.2 mm. Length forecoxa 9 mm. Length forefemur 11mm.

Etymology. Specific epithet from the Greek *pardalotos* meaning spotted like a leopard.

Distribution. Known only from the type locality where the vegetation is primary rain forest (Max Moulds, personal communication). Therefore the species is likely to be rather restricted in Australia but may be expected to occur in New Guinea.

Discussion. Using the keys of Beier (1964, 1968), *Scolodera pardalotus* keys out to family Mantidae, subfamily Mantinae. The spinal formation of the foreleg is fairly typical of that subfamily except that *S. pardalotus* possesses three discoidal spines, a feature shared by only one other genus in the Mantinae, i.e. *Omomantis* Saussure. This feature also appears more or less frequently in almost half of the subfamilies of the Mantidae listed by Beier. The form of the pronotum of *S. pardalotus*, i.e. the two large spiniform tubercles on the metazone of the pronotum is unique among the Mantinae. A similar form of pronotum is found in a group of three apparently related genera, *Mellierella* Giglio-Tos from New Guinea, and *Melliera* Saussure and *Xystropeltis* Rehn from Central America. Giglio-Tos (1927) erected the small subfamily Mellierinae to contain *Melliera* and *Mellierella*, partly on the basis of the bituberculate pronotum. Rehn (1935, 1951) added *Xystropeltis* to this subfamily, however Beier (1935, 1964, 1968) placed these genera in his larger Liturgusinae principally on the basis of the possession of a pit between outer spines 1 and 2 of the forefemur. I have examined two male specimens of *Mellierella biroi* Giglio-Tos one of which has this pit obvious on both femora, the other has the pit fairly obvious on the right femur but not apparent on the left. This feature is completely absent in the holotype of *S. pardalotus*. Further material is needed for study to



Figs 1-6. *Scolodera pardalotus* n.sp., holotype, male. **1:** whole animal, dorsal; **2:** head, anterior; **3:** pronotum, lateral; **4:** right foreleg, inner face.;**5:** genitalia, dorsal; **6:** genitalia, ventral.

determine the variability of this feature and whether the pronotal similarities between *S. pardalotus* and the *Melliera* group indicate true relationship. For the present *S. pardalotus* may tentatively be placed in the Mantinae. Roy (1987) noted that the most recent classification of the Mantodea as a whole (Beier 1964, 1968), is not entirely satisfactory. This may be a case where some rearrangement is necessary.

ACKNOWLEDGEMENTS. I thank Dr D.K. McAlpine of the Australian Museum, Sydney, for the loan of the type specimen; J. Balderson of the ANIC, Canberra for the loan of *Mellierella* specimens; and Dr G. Poore for reading the manuscript.

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The Scopelocheirid Genus *Aroui* (Crustacea: Amphipoda: Lysianassoidea) with Notes on the Association between Scopelocheirid Amphipods, Cassid Gastropods and Spatangoid Echinoids

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Abstract. Formerly *Aroui* was a monotypic scopelocheirid genus known only from the Mediterranean Sea. The type species, *Aroui setosus* Chevreux, is redescribed. It is shown that a neotype, recently established for this species, is invalid, and a lectotype is selected from syntype material in the Muséum National d'Histoire Naturelle, Paris. A second species, *Aroui hamatopodus*, is described, based on widespread collections from the Australian continental shelf and slope. The genus is rediagnosed and distinguished from all other scopelocheirids by two autapomorphic character states. Evidence is presented which suggests that scopelocheirids are very primitive scavengers, and that there is a three-way association between cassid gastropod predators, scopelocheirid amphipod scavengers and their common prey, spatangoid echinoids. An hypothesis is presented which suggests that scopelocheirid scavengers may have evolved by the early Tertiary and that the association involving cassid gastropods and spatangoid echinoids may date from this time.

Lowry, J.K. & H.E. Stoddart, 1989. The scopelocheirid genus *Aroui* (Crustacea: Amphipoda: Lysianassoidea) with notes on the association between scopelocheirid amphipods, cassid gastropods and spatangoid echinoids. Records of the Australian Museum 41(2): 111-120.

Aroui setosus Chevreux, 1911 is well known from the works of Chevreux (1911) and Stroobants (1976). It is the type species of the genus *Aroui* Chevreux which until now was known only from the Mediterranean Sea. Although *Aroui* has been recognised by Stroobants (1976) and Bellan-Santini (1985) as closely related to *Scopelocheirus* Bate, the exact relationship has not been fully understood until now because *Aroui* has been monotypic. Among the extensive collections of lysianassoid amphipods from Australian waters we have found only one species of scopelocheirid lysianassoid, a new species of *Aroui*, which is described below. This has allowed us to rediagnose *Aroui* and consider its relationship to *Scopelocheirus* and other scopelocheirid genera.

Stroobants apparently believed that *A. setosus* was represented by a holotype because she reported being unable to find "la type" in either the Muséum National d'Histoire Naturelle, Paris, (MNHN) or the Musée

Océanographique, Monaco (MOM). She subsequently established a neotype for *A. setosus* from new material collected by E. Dupont in southern Sardinia (Stroobants, 1976:239). However, we believe that all specimens of *A. setosus* from Chevreux's original collection should be regarded as syntypic material, as has always been done by the institutions which hold this material. The designation of a neotype of *A. setosus* by Stroobants is invalid for two reasons. It is contrary to article 75(b)(ii) of the Code of the International Commission on Zoological Nomenclature. *Aroui* is a monotypic genus. Although the species had not been recollected until Stroobants obtained new material from Sardinia, there had been no question concerning its identity. It is easily distinguished from *Scopelocheirus hopei*, its closest relative, and Stroobants apparently had no difficulty identifying *A. setosus* and *S. hopei* in her collections. Thus there were no "exceptional circumstances" or complex zoological problem to justify the establishment of a neotype.

It is contrary to article 75(d)(iii). Stroobants failed to provide reasons for believing the types of *A. setosus* to be lost; syntypes were present at the time in three major institutions, those in the British Museum (Natural History), London and the Musée Océanographique having been reported in the recent literature (Belloc, 1960; Thurston & Allen, 1969).

In 1984 we examined the syntype material of *A. setosus* in the Museum National d'Histoire Naturelle. These specimens are in good condition. We have designated a lectotype, which is registered as Am 3995, from the MNHN Am 900 collection. This specimen is redescribed and illustrated below to allow comparison with the new species. The remaining syntypes (93 in the Museum National d'Histoire Naturelle, Am 900 and 901, 3 in the Musée Océanographique, 3 in the British Museum (Natural History), 1912:4:4:5-7 and 2 in the Australian Museum, Sydney, P35541) become paralectotypes. In accordance with Article 75(h) of the ICZN we referred this matter to the Commission for a ruling and received a reply (P.K. Tubbs, *in litt.*) confirming our interpretation.

Specimens of the new species are deposited in the Australian Museum, Sydney (AM) and the Western Australian Museum, Perth (WAM).

Aroui Chevreux

Aroui Chevreux, 1911: 169.-Barnard, 1969: 328.

Type species. *Aroui setosus* Chevreux, 1911, by monotypy.

Diagnosis. Antenna 1 with well-developed flagellum. Epistome not extending beyond the border of the upper lip; mandibular molar small, cylindrical, triturating; palp article 2 broad proximally, tapering distally. Maxilla 1, outer plate with 11 spine-teeth; inner plate with plumose setae along entire medial margin. Maxilla 2, outer plate half length of inner with long slender, distally barbed setae. Maxilliped outer plate with fully developed apical setae, medial spines and submarginal setae. Coxae 1-4 with setal fringe along ventral margin. Peraeopod 4, coxa with well-developed posteroventral lobe. Peraeopod 5, basis expanded posteriorly, merus expanded posteriorly.

Remarks. We consider scopelocheirids to be very primitive lysianassoids, and *Aroui* and *Scopelocheirus* appear to be the most primitive of the scopelocheirid genera which includes *Bathycallisoma* Dahl, 1959, *Eucallisoma* Barnard, 1961, *Paracallisoma* Chevreux, 1903, *Paracallisomopsis* Gurjanova, 1962 and *Scopelocheiropsis* Schellenberg, 1926. The evidence for this is mainly in the mouthparts. *Aroui* has the following combination of plesiomorphic mouthpart character states which is rarely found among the lysianassoids, but is common in outgroups such as *Valettiopsis* and eusiroids. The lacinia mobilis is a stemmed serrate blade. Plumose setae line the entire margin of the inner plate on maxilla 1. There is little displacement of the spine-teeth on the outer plate of maxilla 1. The outer plate of the maxilliped retains apical plumose setae, well-developed spines along the medial margin and well-developed submarginal setae.

Aroui and *Scopelocheirus* are very closely related as emphasised by Stroobants (1976) and Bellan-Santini (1985). They share two character states, considered to be synapomorphies not found in other scopelocheirid genera: a reduced triturating molar and a proximally broadened article 2 on the mandibular palp. *Aroui* is distinguished from all other scopelocheirid genera by two autapomorphic character states - the reduced outer plate of maxilla 2 with long slender distally barbed setae, and the setal fringe on coxae 1 to 4.

Aroui setosus Chevreux

Fig. 1

Aroui setosus Chevreux, 1911: 170, fig. 3, pl. 7, figs 14-27.-Stroobants, 1976: 239, figs 1-11.-Vader, 1978: 127.

Material examined. Lectotype female, 8.0 mm, ovigerous (8 eggs), MNHN Am 3995; paralectotype female, 7.6 mm, paralectotype male, 5.8 mm, AM P35541 (ex MNHN Am 900); off Bône, north-east of Cap de Garde, Algeria, Mediterranean Sea, [approx. 35°55'N 7°47'E], trawl, on urchins (*Spatangus* sp.), 65 m, E. Chevreux on the yacht *Melita*, 12 June 1904, Stn 726.

Diagnosis. Maxilla 1 palp with 8 terminal spines, 1 flag spine and 1 large subterminal seta. Maxilliped, outer plate with many apical plumose setae. Gnathopod 1 coxa with anterior margin concave, posterior margin straight and ventral margin convex. Gnathopod 2 carpus 3.5 times as long as deep, propodus 2.0 times as long as deep. Peraeopod 6 merus without hooked spines along the posterior margin.

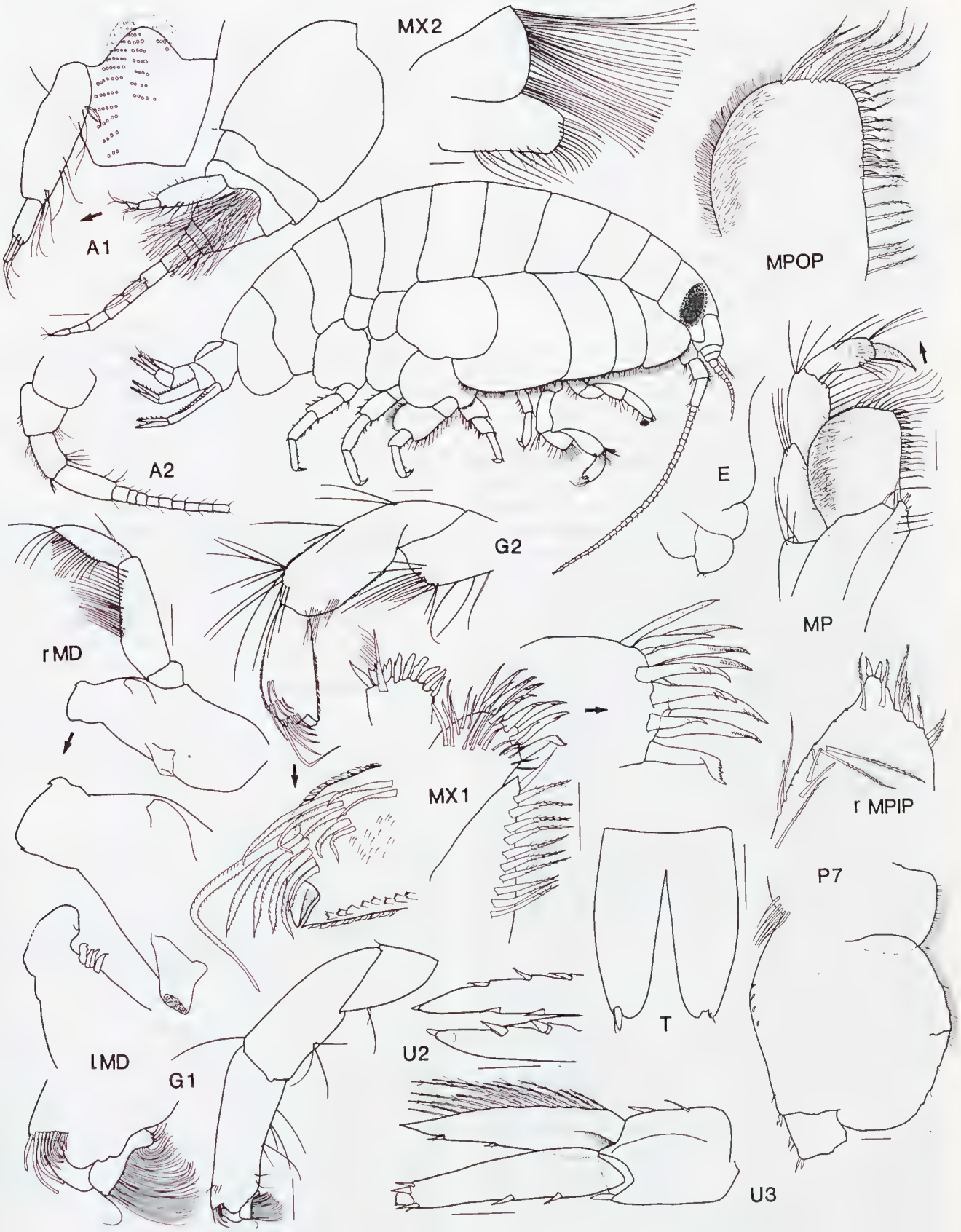

Fig.1. *Aroui setosus* Chevreux, lectotype, female, 8.0 mm, MNHN Am 3995, off Bône, Mediterranean Sea. Scales represent 0.1 mm.

Description. Based on female lectotype, 8.0 mm; dimorphic characters based on male paralectotype, 5.8 mm. *Head* : slightly deeper than long, lateral cephalic lobe well developed, broad, distally truncated; rostrum absent; eyes oval, not enlarged in reproductive male. *Antenna 1*: short, about 0.15 times as long as body, 0.33 times as long as antenna 2; peduncular article 1 short, 1.15 times as long as deep; without midmedial tooth; accessory flagellum 3-articulate, fused proximally to form cap partially covering callynophore; callynophore, well developed 2-field in female and male; flagellum short, 11-articulate; calceoli present in reproductive male. *Antenna 2*: peduncle with brush setae in reproductive male, peduncular articles 4 and 5 not swollen in female or male; flagellum as long as body in reproductive male; calceoli present in reproductive male.

Mouthpart bundle: subquadrate. *Epistome and upper lip*: separate, subequal. *Mandible*: incisors symmetrical, both with slightly convex margins; left lacinia mobilis present, a stemmed serrate blade; accessory spine row, left with 3 stout spines; right with 3 spines (obscured); molar with narrow column, weak triturating surface; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, broadened proximally, tapering distally, with 22 setae along 0.7 of distal medial margin; article 3 weakly falcate with 4 E-setae, 18 D-setae along most of posterior margin, and 1 B-seta. *Maxilla 1*: inner plate tapering distally, inner margin with 11 plumose setae along entire inner margin; outer plate narrow, with 11 spine-teeth in 2 rows, outer row with 7 spine-teeth, large, slender, distally multicuspidate, inner row with 4 spine-teeth, spine-tooth 1 large, slender, smooth, spine-teeth 2-3 large, slender, 3- and 2-cuspidate, spine-tooth 4 short, slender, with 1 cusp; palp large, 2-articulate, with 8 terminal spines, 1 flag spine and 1 subterminal seta. *Maxilla 2*: outer plate broad, half length of inner plate, with long slender distally barbed setae. *Maxilliped*: inner plate large, subrectangular, with 2-3 well-developed nodular spines, oblique setal row well developed, with 12 plumose setae and a submarginal row of 6 plumose setae; outer plate large, subovate, with 9 apical plumose setae, apical spines absent, 11 medial spines present, 17 marginal setae present; palp well developed, dactylus well developed, unguis present, terminal setae absent.

Gnathopod 1: simple; coxa 1 large, anterior margin concave, forming anteroventrally produced corner, posterior margin straight, ventral margin setose; carpus subrectangular, 3.0 times as long as deep, posterior margin straight, subequal in length to propodus; propodus large, subrectangular, 3.0 times as long as deep, margins subparallel; posterior margin smooth, subtly sinuate, without spines; dactylus extremely reduced and covered in sensory setae. *Gnathopod 2*: minutely chelate; coxa large, subequal in size to coxa 3, ventrally setose; carpus elongate, 3.5 times as long as deep, posterior margin straight; propodus subrectangular, short, 2.0 times as long as deep; palm obtuse, with straight margin; posterodistal corner with 1 medial spine.

Peraeopods 3-7: with short, stocky dactyli. *Peraeopod 3*: coxa large. *Peraeopod 4*: coxa with well-developed posteroventral lobe, anterior and posterior margins subparallel; male merus/carpus without setal brushes. *Peraeopod 5*: coxa bilobate, posterior lobe not produced ventrally; basis broadly expanded with posterior margin rounded; merus broadly expanded and posteriorly setose. *Peraeopod 6*: merus slightly expanded, posterior margin without setae; propodus, posterior margin without hooked spines. *Peraeopod 7*: basis, posterior margin slightly rounded with rounded posteroventral corner and rounded posteroventral margin; merus slender, not expanded posteriorly. *Oostegites:* from gnathopod 2 to peraeopod 5. *Gills*: from gnathopod 2 to peraeopod 7, smooth, gill on peraeopod 7 not reduced.

Epimeron 3: with broadly rounded posteroventral corner.

Uropod 1: rami subequal in length. *Uropod 2*: rami subequal in length, outer ramus without constriction. *Uropod 3*: peduncle short, 1.3 times as long as deep, without lateral flange; rami lanceolate; outer ramus 2-articulate; rami subequal in length; plumose setae present in female and male. *Telson*: longer than broad, deeply cleft (80%), without dorsal spines, distal margins rounded, with 1 simple seta and 1 spine apically on each lobe.

Remarks. *Aroui setosus* and *A. hamatopodus* are very similar. They differ mainly in the shape of coxa 1 which has a concave anterior margin in *A. setosus* and is convex in *A. hamatopodus*, and in the presence of hooked spines on the propodus of peraeopod 6 in *A. hamatopodus*.

Distribution. Apparently *Aroui setosus* is confined to the Mediterranean Sea.

Aroui hamatopodus n.sp.

Figs 2-4

Scopelocheirus sp. McNamara & Henderson, 1984: 410.

Type material. HOLOTYPE, male, 7.8 mm, AM P38460; PARATYPE female, 8.0 mm with oostegites, AM P38461; 9 PARATYPES AM P38462; from the stomach of a jackass fish, *Nemadactylus macropterus*, New South Wales waters, 73-183 m, A.C.S., July 1939.

Additional material examined. NEW SOUTH WALES: 1 specimen, AM P38463, east of Long Nose Point, 33°42'S 151°55'E, 620 m, 11 Dec. 1978, RV *Kapala* Stn K78-27-02. VICTORIA: 1 specimen, NMV J15062, South of Point Hicks, 38°17.7'S 149°11.3'E, coarse sand, gravel, mud, many sponges, 400 m, 24 July 1986, RV *Franklin* Slope Stn 40. WESTERN AUSTRALIA: 14 specimens, AM P38465, 129 specimens, WAM 38-84, north-east of Rowley Shoals, 16°56'S 120°06'E, feeding on a recently killed test of a large spatangoid, *Taimanawa mortenseni* Henderson & Fell, 431 m, 20 Aug. 1983, FV *Courageous*. QUEENSLAND: 10 specimens, AM P38464, North-east of Lady Elliot Island, 24°03.7'S 152°49.9'E, rubble bottom with many small disk corals, 150 m, 4 July 1984, HMAS *Kimbla* Stn 3.

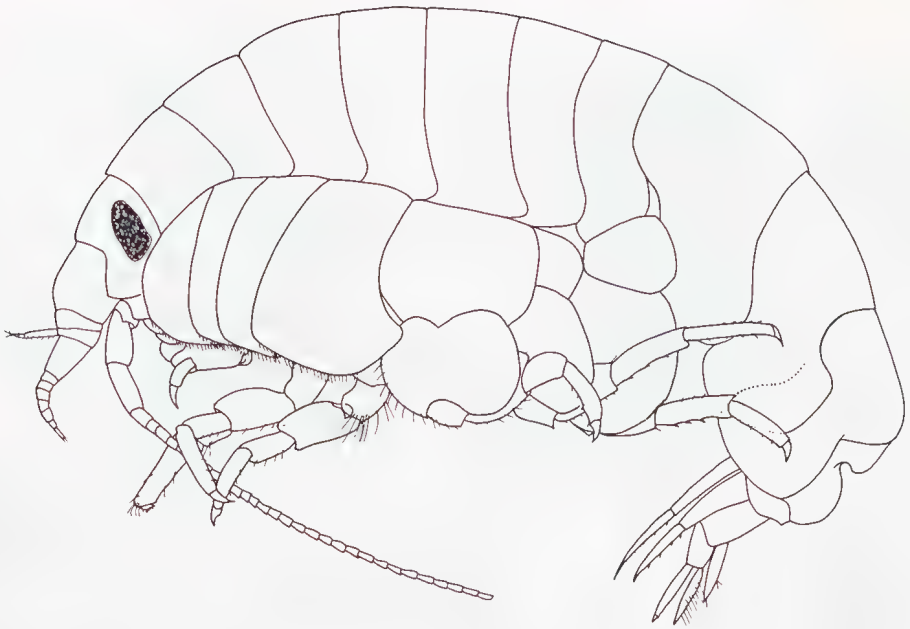

Fig.2. *Aroui hamatopodus* n.sp., holotype, male, 7.8 mm, AM P38460, New South Wales, Australia.

Diagnosis. Maxilla 1 palp with 6 terminal spines, 1 flag spine and 1 subterminal seta. Maxilliped, outer plate with 2 apical plumose setae. Gnathopod 1 coxa with anterior margin convex, posterior margin straight and ventral margin convex. Gnathopod 2 carpus 2.5 times as long as deep, propodus 1.6 times as long as deep. Peraeopod 6 merus with 6 hooked spines along the posterior margin.

Description. Based on holotype male (AM P38460), 7.8 mm and a paratype female (AM P38461), 8.0 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, broad, distally rounded; rostrum absent; eyes oval, not enlarged in reproductive male. *Antenna 1*: short, about 0.17 times as long as body, 0.3 times as long as female antenna 2; peduncular article 1 short, 0.87 times as long as deep; without midmedial tooth; accessory flagellum 3-articulate, fused proximally to form cap partially covering callynophore; callynophore, well-developed 2-field in female and male; flagellum short, 9-articulate; calceoli present in reproductive male. *Antenna 2*: peduncle with brush setae in reproductive male, peduncular articles 4 and 5 not swollen in female or male; flagellum about half as long as body in reproductive male; calceoli present in reproductive male.

Mouthpart bundle: subquadrate. *Epistome and upper lip*: separate, subequal. *Mandible*: incisors symmetrical, both with slightly convex margins; left lacinia mobilis a stemmed serrate blade; accessory spine row, left and right each with 3 stout spines; molar with narrow column, weak triturating surface; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, broadened proximally, tapering distally, with 18 setae along 0.66 of distal medial margin; article 3 weakly falcate with 4 E-setae, 11 D-setae along most of posterior margin, and 1 B-seta. *Maxilla 1*: inner plate tapering distally, with 11 plumose setae along entire inner margin, outer plate narrow, with 11 spine-teeth in two rows, outer row with 7 spine-teeth (spine-tooth 1 slightly displaced onto inner row), large, slender, distally multicuspidate, inner row with 4 spine-teeth, spine-teeth 1-2 large, slender, multicuspidate, spine-tooth 3 large, slender, 2-cuspidate, spine-tooth 4, small, with 1 cusp; palp large, 2-articulate, with 6 terminal spines, 1 flag spine and 1 subterminal seta. *Maxilla 2*: outer plate broad, half length of inner plate, with long, slender, distally barbed setae. *Maxilliped*: inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row well developed, with 12 plumose setae; outer plate large, subovate, 2 apical plumose setae present, 11 submarginal plumose setae present, 12 medial spines present, palp well developed, dactylus well developed, unguis present, terminal setae absent.

Gnathopod 1: simple; coxa 1 large, anterior margin convex, posterior margin straight, ventral margin convex, setose; carpus subrectangular, 2.5 times as long as deep, posterior margin straight; 0.86 times as long as propodus; propodus large, subrectangular, 3.0 times as long as deep, margins subparallel; posterior margin smooth, subtly sinuate, without spines; dactylus extremely reduced and covered in sensory setae. *Gnathopod 2*: minutely subchelate; coxa large, subequal in size to coxa 3, ventrally setose; carpus elongate, 2.5 times as long as deep, posterior margin straight; propodus subrectangular, short, 1.6 times as long as deep; palm obtuse, with rounded margin; posterodistal corner with 1 lateral and 1 medial spine.

Peraeopods 3-7 with short, stocky dactyli. *Peraeopod 3*: coxa large, ventrally setose. *Peraeopod 4*: coxa ventrally setose with well-developed posteroventral lobe, anterior and posterior margins subparallel; male merus/carpus without setal brushes. *Peraeopod 5*: coxa bilobate, posterior lobe not produced ventrally; basis broadly expanded with posterior margin rounded; merus broadly expanded and posteriorly setose. *Peraeopod 6*: merus slightly expanded without posteriorly setose margin;

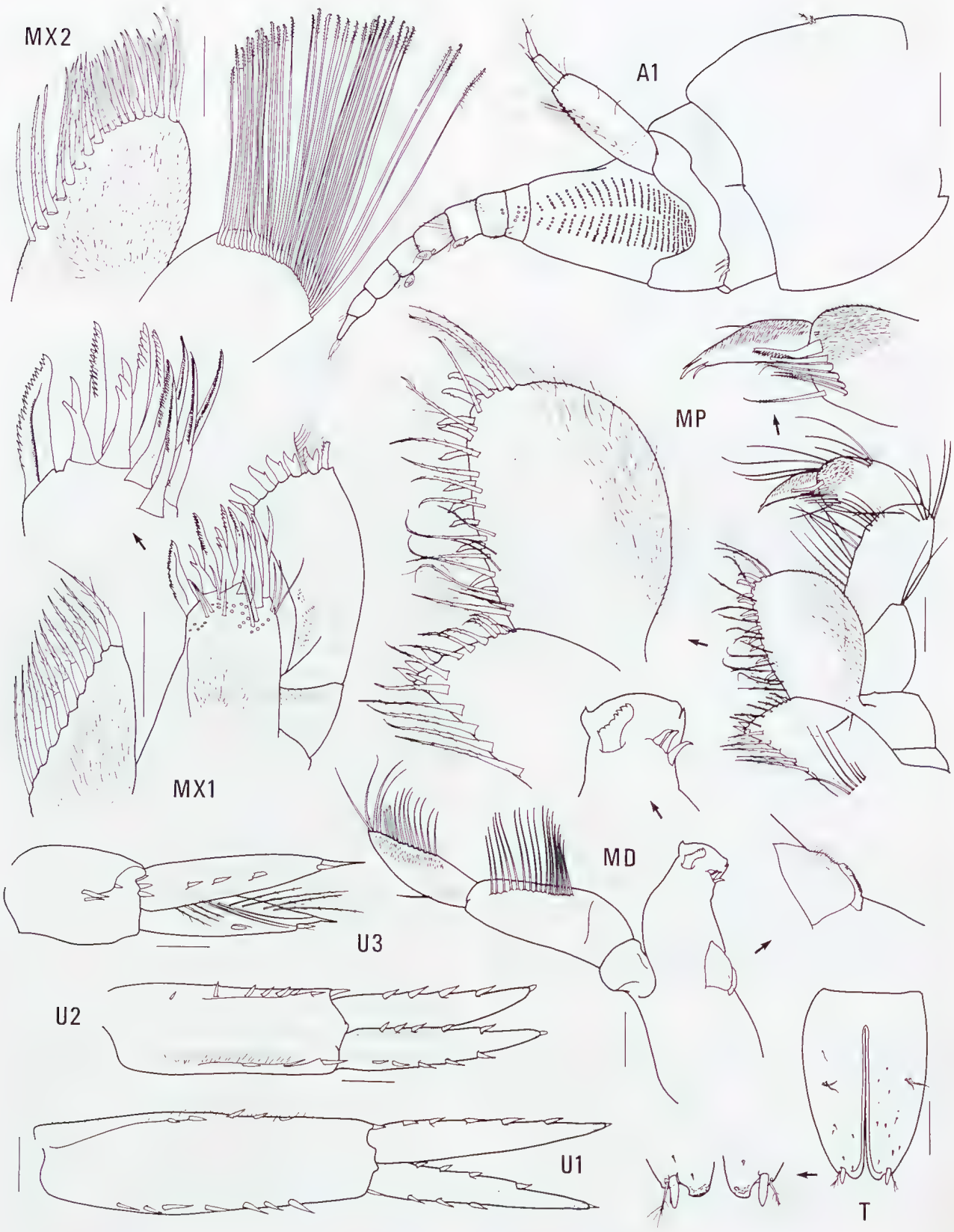

Fig.3. *Aroui hamatopodus* n.sp., holotype, male, 7.8 mm, AM P38460, New South Wales, Australia. Scales represent 0.1 mm.

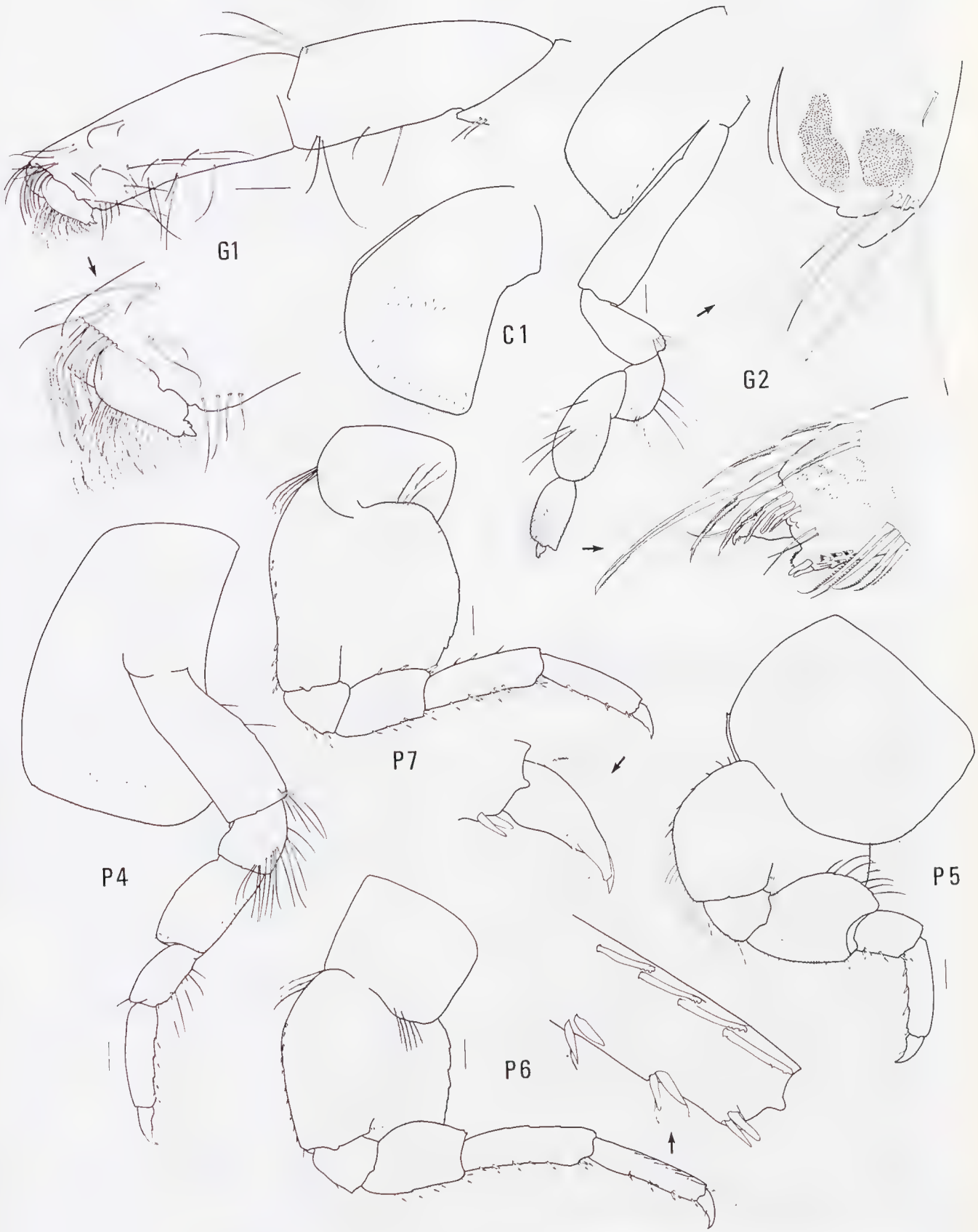

Fig.4. *Aroui hamatopodus* n.sp., holotype, male, 7.8 mm, AM P38460, New South Wales, Australia. Scales represent 0.1 mm.

propodus, posterior margin with 6 hooked spines. *Peraeopod 7*: basis, posterior margin slightly rounded with rounded posteroventral corner and rounded posteroventral margin; merus slender, not expanded posteriorly. *Oostegites*: from gnathopod 2 to peraeopod 5. *Gills*: from gnathopod 2 to peraeopod 7, smooth, gill on peraeopod 7 not reduced.

Epimeron 3: with a broadly rounded posteroventral corner.

Uropod 1: rami subequal in length. *Uropod 2*: rami subequal in length, outer ramus without constriction. *Uropod 3*: peduncle short, 1.3 times as long as deep, without lateral flange; rami lanceolate; outer ramus 2-articulate; rami subequal in length; plumose setae present in female and male. *Telson*: longer than broad, deeply cleft (80%), distal margins rounded, without dorsal spines, with 1 simple seta and 1 spine apically on each lobe.

Etymology. The specific name alludes to the peculiar hooks on the propodus of peraeopod 6.

Remarks. For the relationship of *Aroui hamatopodus* to *A. setosus* see the remarks for the latter species.

Distribution. *Aroui hamatopodus* is known from the outer continental shelf of north-western Australia, and the continental shelf and slope from north-eastern to south-eastern Australia.

The Association between Scopelocheirid Amphipods, Cassid Gastropods and their Common Prey, Spatangoid Echinoids

Scopelocheirids, spatangoid scavengers. Chevreux's (1911) original material of *A. setosus* was collected on a spatangoid echinoid *Spatangus* sp. Stroobants (1976) reported two large collections of *A. setosus*, each inside the test of *Spatangus purpureus* O.F. Muller. McNamara & Henderson (1984) reported *A. hamatopodus* (as *Scopelocheirus* sp.) feeding inside the test of the spatangoid *Taimanawa mortenseni* Henderson & Fell. Stroobants also recorded *A. setosus* from the sponge *Suberites* covering a gastropod shell which housed a hermit crab, *Paguristes oculatus* (Fabricius).

Species of *Scopelocheirus*[1] have also been reported in association with spatangoids. Costa (1852) reported *Scopelocheirus hopei* Costa, sometimes in extraordinary numbers in the tests of spatangoids in the Gulf of Naples. Wrzesniowski (1874) reported *S. branickii* Wrzesniowski in the clypeasteroid *Clypeaster* sp. (almost certainly misidentified and possibly a spatangoid: Rowe, personal communication), from Nice. Metzger (1875) reported *S. kroyeri* (Bruzelius) in great numbers within a dead specimen of the spatangoid *Echinocardium cordatum* (Pennant) among collections from the Firth of Forth, Scotland. Robertson (1888) reported *S. crenatus* Bate in a partly broken test of *Brissopsis lyrifera* (Forbes) from Liverpool Bay, England, a phenomenon he observed more than once. Chumley (1918) also reported *S. crenatus* from *Brissopsis lyrifera* in the Clyde Sea area. Chevreux & Fage (1925) recorded *S. hopei* from *Spatangus* sp. in the Mediterranean Sea. Stephensen (1935) cited a report of *S. hopei* inside the empty tests of *Echinocardium cordatum* from Plymouth, England. Stroobants (1976) recorded *S. hopei* and *A. setosus* inside the same test of *S. purpureus* from collections made off Cape Ferrato and Torre Corallo, Sardinia, Mediterranean Sea. Moore (1984) recorded *S. hopei* from tests of dead *Brissopsis lyrifera* in the Clyde Sea area.

Species of *Scopelocheirus* have also been recorded as scavengers on other food sources. Sars (1890) reported *S. crenatus* as plentiful in Trondheimsfjord from dead fish fastened to fishermen's lines. Monod (1923) found *S. hopei* swarming in thousands on the carcasses of fish taken off Cap d'Ail in the Mediterranean. Chevreux (1895) recorded *S. hopei* attacking specimens of the lysianassoid amphipod *Ichnopus affinis* Heller taken in traps off Monte-Cristo, and noted that they also voraciously attacked fish in the nets of fishermen becalmed at sea. Chevreux noted that *S. hopei* attacked *I. affinis* from the ventral part of the thorax and gained entry by a break made between the fifth and sixth segments. This may explain Stroobants' (1976:256) observation of seven instances where a juvenile of *S. hopei* was found in the "poche incubatrice" of *A. setosus*. It seems highly probable that the young *S. hopei* were actually attacking and eating individuals of *A. setosus*. Scott (1900) reported *S. crenata* burrowing into the flesh of the tope shark *Galeus canis* Bonaparte (= *Galeorhinus galeus* Linnaeus) taken off Aberdeen, Scotland. Similar occurrences have been reported by Williams (1938) and Moore (1984). Williams found *S. hopei* eating the gills, eye muscles and associated nerves of the dogfish *Acanthias vulgaris* (= *Squalus acanthias* Linnaeus) taken on long lines off the north-eastern coast of Ireland. Moore found large numbers of *S. hopei* attacking dead dogfish *Scyliorhynus cunicula* Linnaeus on baited lines in the Clyde Sea area, and also from traps baited with crab meat. Sekiguchi & Yamaguchi (1983) reported *S. hopei* collected from deep water off east central Japan in traps baited with fish.

Vader (1978) suggested that *Aroui setosus* was a scavenger on *Spatangus* and that species of *Scopelocheirus* were more generalised scavengers with a preference towards spatangoids. We consider that species of *Aroui* are likely to be exclusive scavengers of spatangoids and that species of *Scopelocheirus* behave as suggested by Vader.

McNamara & Henderson (1984) have explained a mechanism by which scopelocheirids may gain access to the inside of echinoids. In their specimen of *Taimanawa mortenseni* and in another specimen of *T. pulchella* Henderson & Fell there was "...a prominent circular hole in the anterior of the adoral surface of the test." They suggested that both specimens "...were probably attacked and killed by predatory gastropods..." and that the amphipods "...were probably scavenging a recently killed

[1]Because of the uncertainty concerning the taxonomic status of species in the genus *Scopelocheirus* we are using species names as given in the original reports.

individual." This observation indicates one way in which amphipods can enter a spatangoid test and may explain some earlier records where large numbers of scopelocheirids were found inside spatangoid tests.

Cassids, spatangoid predators. The mesogastropod family Cassidae feeds almost exclusively on echinoids (Hughes & Hughes, 1981). They drill a hole in the wall of the prey, insert the proboscis and eat everything but the gut. The hole is indistinguishable from the hole observed by McNamara & Henderson (1984) in their specimen of *Taimanawa mortenseni* the same specimen from which *Aroui hamatopodus* was taken. Cassids live predominantly on sandy substrates in tropical or warm temperate environments (Hughes, 1986). However species in the genus *Galeodea* tend to occur in deep cool water (O'Riordan, 1966, 1971; Ponder, 1983). Hughes (1986) has described in detail the feeding mechanisms of *Galeodea echinophora* (Linnaeus) on *Echinocardium cordatum*, both of which occur together in the Mediterranean Sea. *Scopelocheirus kroyeri* and *S. crenatus* have both been recorded from inside *Echinocardium cordatum* (Metzger, 1875; Stephensen, 1935). Ponder (1983) has recently described *Galeodea maccamleyi* from off the Queensland coast in depths of 220 to 365 m. Several large species of *Phalium*, another cassid genus known to feed on burrowing echinoids, are present in the collections of the Australian Museum and the Western Australian Museum from deep water (350 to 500 m) in Queensland and Western Australian. Thus there are several potential cassid predators of *Taimanawa mortenseni* in Australian waters.

However this may not be the only way in which species of *Aroui* and *Scopelocheirus* subsist. Hughes (1986) reported that when a *Galeodea* abandons an *Echinocardium* "...the test is stripped of all tissues except the gut, which was often burst and showed signs of lysis." In one species, *Aroui setosus*, the amphipod is identical in colour to the echinoid with which it is associated. It is possible that the scopelocheirids live in some other capacity among the spines of the echinoid host and scavenge it when the echinoid dies or is killed by a predator such as a cassid.

Fossil evidence. The majority of records report *Aroui* and *Scopelocheirus* associated with the spatangoid genera *Brissopsis*, *Echinocardium*, *Spatangus* and *Taimanawa*. These records are widespread geographically - the North Atlantic Ocean, the Mediterranean Sea and the eastern Indian Ocean - and imply a Tethyan distribution with post Tethyan speciation. All of the spatangoid genera associated with scopelocheirids are known from the fossil record (Mortensen, 1951; Henderson & Fell, 1969). *Spatangus* and *Taimanawa* are known from the Eocene, *Echinocardium* is known from the Oligocene and *Brissopsis* is known from the Miocene. Related spatangoid genera are known from the Mesozoic. Cassids first appear in the Cretaceous and there is evidence of cassids preying on echinoids in the Eocene (Sohl, 1969).

There is no lysianassoid fossil record, but based on the peracaridan fossil record amphipods may have arisen in the Carboniferous (Bousfield, 1978). Scopelocheirids have many plesiomorphic character states and may be among the earliest known lysianassoid scavengers. The potential for an association with spatangoids therefore extends back to the early Tertiary.

A possible origin of scavenging. It is possible that a commensal lysianassoid similar to an *Aroui* began to eat its host when the host died. Probably it gained access through the mouth or the anus and fed on the relatively soft tissue without highly modified mouthparts. Subsequent lysianassoids remained associated with the host, also feeding on it when it died. But these animals began to scavenge on other kinds of dead animals. Eventually some lysianassoids became free living and began to scavenge on a variety of dead animals. In these lysianassoids the mouthparts became highly modified for cutting the firm tissue of animals such as fish (Thurston, 1979).

There has been a proliferation of scavenging lysianassoids, particularly in cooler seas and in the deep sea. Genera such as *Alicella*, *Anonyx*, *Eurythenes*, *Ichnopus*, *Orchomene* and *Podoprion* belong in various, yet to be defined, lysianassoid family groups; but all have species reported as scavengers. Most of these animals are free living and all have some degree of modification in the mouthparts. The phylogenetic relationships between these groups and the scopelocheirids are unknown.

Conclusions. We suggest that scopelocheirids are specialised scavengers on spatangoid echinoids; that cassid gastropods provide one means by which scopelocheirids gain access to spatangoid tests; that there is a three-way association between the cassid predator, the spatangoid prey and the scopelocheirid scavenger; that the association may extend back at least to the Tertiary; and that the association between *Aroui* and the spatangoids may give us an indication of how scavenging evolved.

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Early Devonian Conodonts from the Kuan Tung Formation, Thailand: Systematics and Biogeographic Considerations

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Abstract. A small conodont assemblage, obtained from a limestone marking the boundary between the middle and upper units of the Kuan Tung Formation, Satun Province, South Thailand, contains *inter alia* *Pandorinellina steinhornensis steinhornensis*, *Polygnathus labiosus mawsonae* n.subsp., and *Pseudooneotodus kuangtungensis* n.sp., indicating an Emsian age (*perbonus-serotinus* Zones). Studies on ontogenetic variation in Pa elements of *Polygnathus labiosus mawsonae* n.subsp. show that smaller Pa elements have fewer transverse ridges on the posterior third of the platform, more distinct marginal denticulation on the platform and a proportionately smaller basal cavity. The basal cavity lips may break off in mature specimens; this gives an appearance of a small basal cavity. The distribution of *P. labiosus*, *P. pseudoserotinus*, *P. perbonus* and *Pseudooneotodus kuantungensis* n.sp., in the Shan-Thai and South China Terranes, together with supporting evidence from thelodontid and placoderm fishes, suggests that these terranes were in close proximity to the eastern margin of Gondwana at the end of the Early Devonian.

Long, J.A. & C.F. Burrett, 1989. Early Devonian conodonts from the Kuan Tung Formation, Thailand: systematics and biogeographic considerations. Records of the Australian Museum 41(2): 121-133.

Little is known of the Devonian conodont faunas from south-east Asia compared to the vast amount of data from Europe, America and Australia. Conodont faunas from Thailand have been listed by Baum *et al.* (1970) and Bastin *et al.* (1977) for isolated localities in the north of the country. Most of these are of Early Devonian age, except for two sites yielding Givetian and Famennian conodonts. None of the localities are from specifically named lithological units, and their stratigraphic relationships are uncertain. Burrett *et al.* (1987) described a limited conodont fauna from the Mae Ping Formation, south of Chiang Mai, establishing a Siluro-Devonian age for a sequence previously thought to be Ordovician. Fortey (in press) reports that a few conodonts including *Icriodus* sp. and *Polygnathus* sp. were recovered from chippings of limestone from preparation of trilobites from Satun Province in the south of Thailand. These come from the same stratigraphic section as the fauna described herein. No icriodids were recovered from

our samples.

The Shan-Thai Terrane (*sensu* Burrett & Stait, 1987) incorporates the eastern side of Burma, the western half of Thailand, parts of Malaysia, the west of Yunnan Province, China, and the small area of Laos between these regions (Fig. 1). Our knowledge of Devonian conodonts from within these boundaries is still small but information from all known assemblages collectively builds up a scenario of the Shan-Thai Devonian conodont fauna. Lane *et al.* (1979, also Alexander & Müller 1963) documented Early-Late Devonian conodont faunas from Batu Gajah, near Perak, Malaysia (Fig. 1), and Metcalfe (1983) described one element of *Polygnathus linguiformis* s.s. from near this area. To date, no conodonts have been described from Burma or the Shan-Thai region of Laos. Recently Wang *et al.* (1986) described Middle Devonian thelodont scales from Shidian, Western Yunnan (Fig. 1) and listed the major conodont species occurring in the section, from Lower Devonian (*serotinus* Zone) to the base of the Upper Devonian (*asymmetricus* Zone) in age.

Conodonts studied in this paper were obtained from a limestone horizon in the Kuan Tung Formation, Satun Province during fieldwork by Burrett & Wongwanich in 1987. The complete stratigraphic section, with precise locality details for measured stratigraphic sections, has been described by Wongwanich *et al.* (in press), and has been designated a type section for the Devonian in South Thailand. Many samples have been taken for detailed biostratigraphic work, but the results of these studies will not be available for some time. This work describes a limited conodont fauna of some 114 elements collected from the Kuan Tung Formation and discusses the biogeographic implications of the fauna. The precise locality of the sample is from an exposure of the Kuan Tung Formation in a pararubber plantation 10 km north of Langu (grid ref. 7000, 8500, Amphoe Langu 1:50,000 sheet).

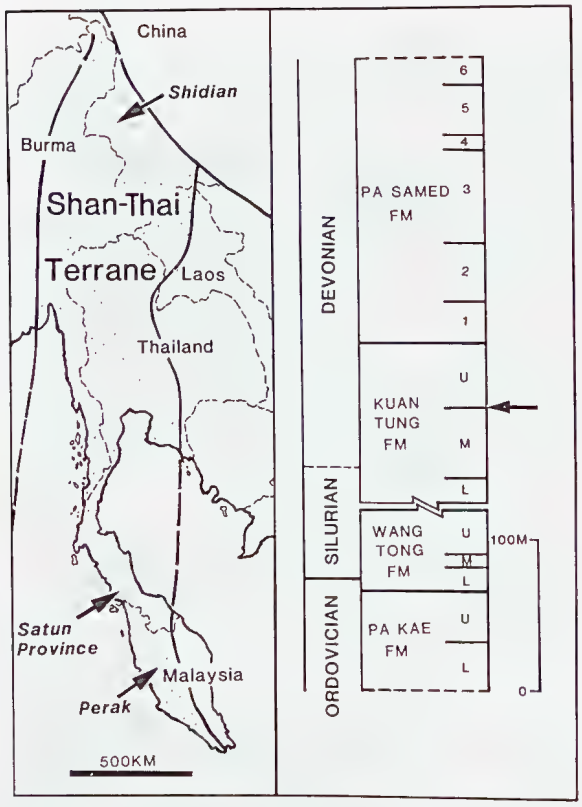

Fig.1. Map showing boundaries of Shan-Thai Terrane and localities mentioned in text. Part of the stratigraphic column of Satun Province is shown on the right with an arrow indicating the horizon where the conodont sample was collected.

Systematic Palaeontology

Only the Pa elements of polygnathids are described. Specimens are housed in the collections of the Geology Department, University of Tasmania (UTGD). All material was photographed by the Scanning Electron Microscope with tilt adjustments correcting optical distortions.

Belodella (Pander, 1856)

Belodella devonica Stauffer

Figs 2.4, 2.6

Remarks. Few specimens are well preserved, but all of them show the biconvex cross-section and gently tapering shape characteristic of this species.

Material examined. 9 specimens (UTGD 123739-123747).

Belodella resima (Philip 1965)

Figs 2.1

Remarks. This species is identified by the triangular cross-section and well-defined crista bordering the outer margin. The illustrated specimen shows the characteristic strongly incurved tapering point.

Material examined. 3 specimens (UTGD 123748 - 123750).

Drepanodus Pander, 1856

Drepanodus sp.

Figs 2.2, 2.3, 2.5

Remarks. These drepanodiform elements are characterised by their compressed basal cross-section and slightly flared base.

Material examined. 5 specimens (UTGD 123713-715; 123753-754).

Fig.2. 1, *Belodella resima* (Philip), UTGD 123478, x57. 2, 3, 5, *Drepanodus* sp. 2, UTGD 123753, x70; 3, UTGD 123713, x143; 5, UTGD 123714, x131. 4, 6, *Belodella devonica* Stauffer. 4, UTGD 123739 x50; 6, UTGD 123740, x126. 7, *Panderodus* sp., UTGD 123756, x140.

Panderodus Ethington, 1959

Panderodus sp.

Fig. 2.7

Remarks. The few, incomplete specimens in the material resemble *P. acostatus* in the cusp being gently recurved and lacking the longitudinal carina seen in *P. unicostatus*. The lateral faces are somewhat rounded and the base of the unit is compressed in cross-section.

Material examined. 2 specimens (UTGD 123755-756).

Pandorinellina Müller & Müller, 1957

Pandorinellina steinhornensis steinhornensis (Ziegler, 1956)

Fig. 3, Fig. 4.1, 4.2, 4.5, 4.6, 4.10.

Remarks. This species is readily identified by the even denticulation of the blade and the widely flared, asymmetric basal cavity located closer to the posterior half of the unit. Lane *et al.* (1979) noted a new subspecies of *P. steinhornensis* from Perak, Malaysia, occurring in the *gronbergi-dehiscens* Zones. Our specimens, however, differ from the Malaysian subspecies in having a broader basal cavity in an off-central position along the blade. One specimen (Fig. 4.5, 4.6) has a more rounded basal cavity outline than all others, but in other respects falls within the normal range of variation for the species. In Australia *P. steinhornensis steinhornensis* has been recorded from the Lilydale Limestone (Philip & Pedder 1967); however these specimens have a large basal cavity which extends to the posterior end.

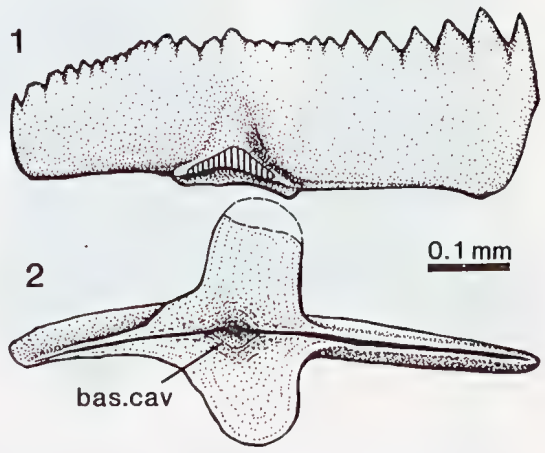

Fig.3. *Pandorinellina steinhornensis steinhornensis*, typical morphotype from Kuan Tung Fm, UTGD 123680. bas.cav - basal cavity.

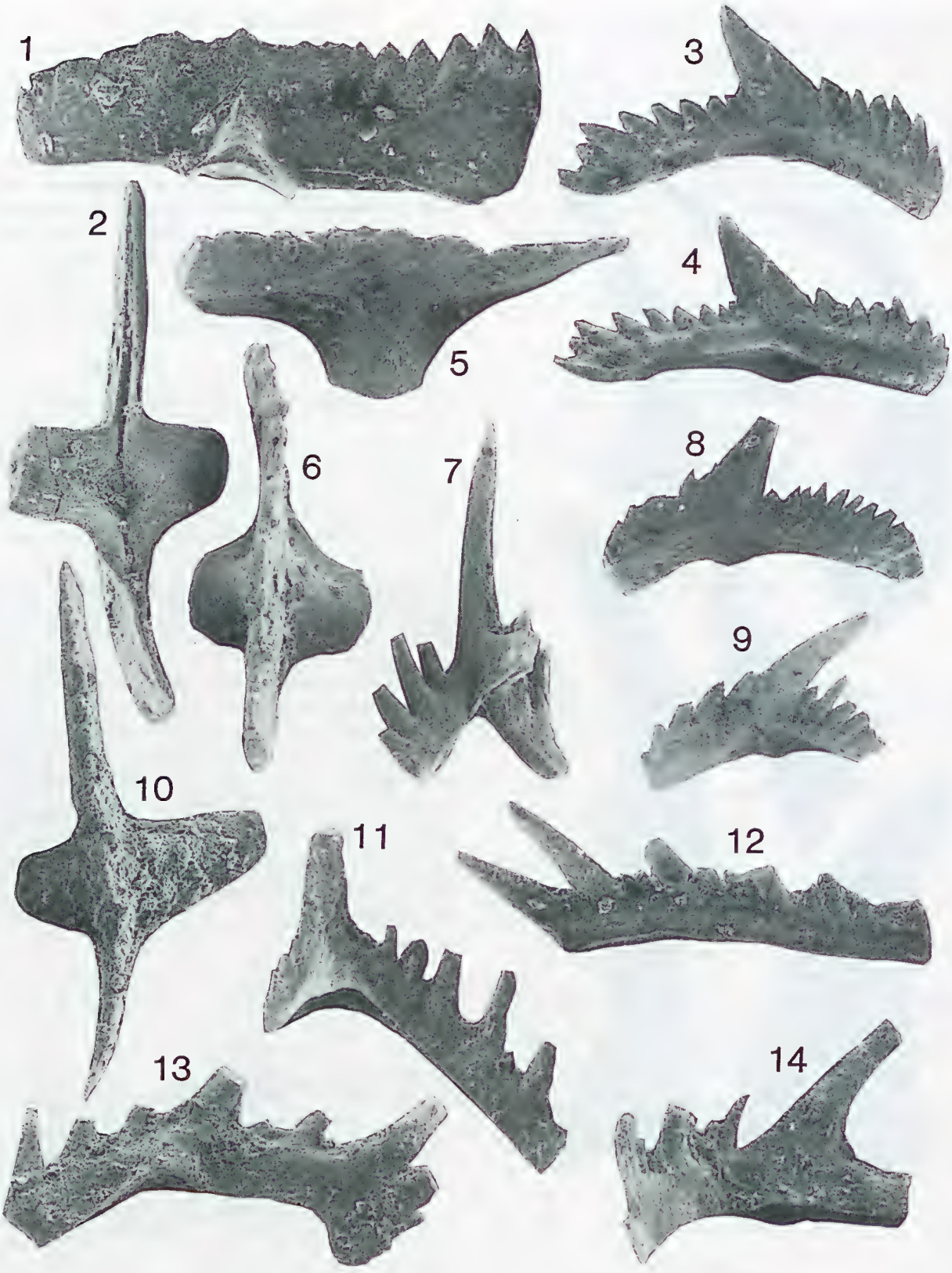

Fig.4. 1, 2, 5, 6, 10. *Pandorinellina steinhornensis steinhornensis*. 1, 2, UTGD 123680, x 150. 5, 6, UTGD 123682, x 170. 10, UTGD 123679, x 170. Unassigned polygnathid and ozarkodinid elements: Pb elements -3, 4, UTGD 123697, x 140; 8, UTGD 123698, x 140; 9, UTGD 123699, x 140. Sa element - 7, UTGD 123702, x 140. M element - 11, UTGD 123706, x140. Sc element - 12, UTGD 123705, x 140. Sb elements - 13 (polygnathid), UTGD 123701, x 150; 14 (ozarkodinid), UTGD 123707, x 140.

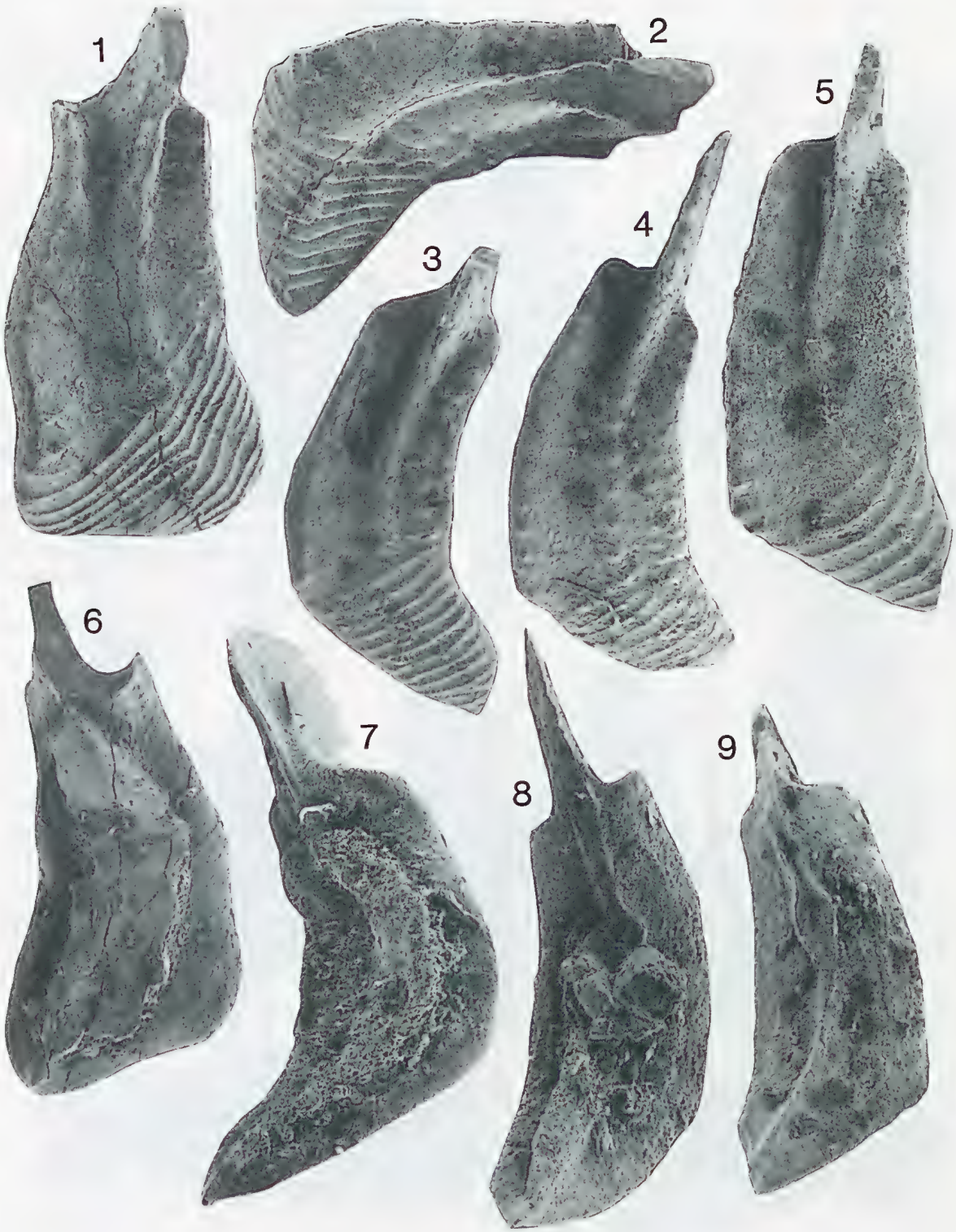

Fig.5. *Polygnathus labiosus mawsonae* n.subsp. 1, 2, 6, paratype UTGD 123643, x 76 (lips of basal cavity well preserved). 3, 7, holotype UTGD 123642, x 78 (anterior region of free blade damaged during handling: absent in 3); 4, 8, paratype UTGD 123644, x 78 (lips of basal cavity partially broken off); 5, 9, paratype UTGD 123645, x 101 (lips of basal cavity completely broken away).

Material examined. 11 specimens (UTGD 123672-682).

Polygnathus Hinde, 1879

Remarks. Klapper (*in* Ziegler, 1973) discussed the genus, and Mawson (1987a) reviewed the Australian Lower Devonian species.

Polygnathus labiosus Mawson 1987a

Polygnathus labiosus mawsonae n.subsp.

Figs 5, 6, 7

Etymology. For Dr Ruth Mawson, Macquarie University, Sydney.

Diagnosis. Pa elements of *P. labiosus* in which the posterior third of the platform is particularly broad and is ornamented with closely-spaced parallel transverse ridges which rarely bifurcate; the anterior margin of the platform is narrower than the broadest part of the posterior end of the platform; and the inner and outer margins have weak denticulation. The basal cavity has a rounded anterior margin.

Material examined. 30 specimens. HOLOTYPE: UTGD 123642 [Fig. 5(3,7); Fig. 6(1,2)]. PARATYPES: UTGD 123643 [Fig. 5(1,2,6); Fig. 6(3)], UTGD 123644 [Fig. 5(4,8)], UTGD 123645 [Fig. 5(5,9)], UTGD 123646. Other material UTGD 123647-123671, plus several unregistered broken Pa elements.

Remarks. The Pa elements of this species are identified by the flaring lips on the large relatively flat to concave basal cavity with the basal aperture situated well anterior of the strong inward deflection of the platform. The flared lips are not basal filling but true extensions of the basal cavity rims.Close examination of the lips shows that the surface is smooth and lacking the spongiose texture of basal filling, and that when a specimen is dissected the cross-section shows the outward extension of the rims of the basal cavity.The outer margin is strongly convex.The carina (car, Fig. 6) is weakly developed on the platform and ends about halfway along the the platform. The posterior half of the platform has gently convex margins. The outer platform anterior margin is lower than that of the inner platform. The ornamental ridges on the inner and outer platform margins are weakly developed, and there is a broad smooth area between the end of the carina and the posterior region of the outer platform.

Our specimens differ from those figured from the type

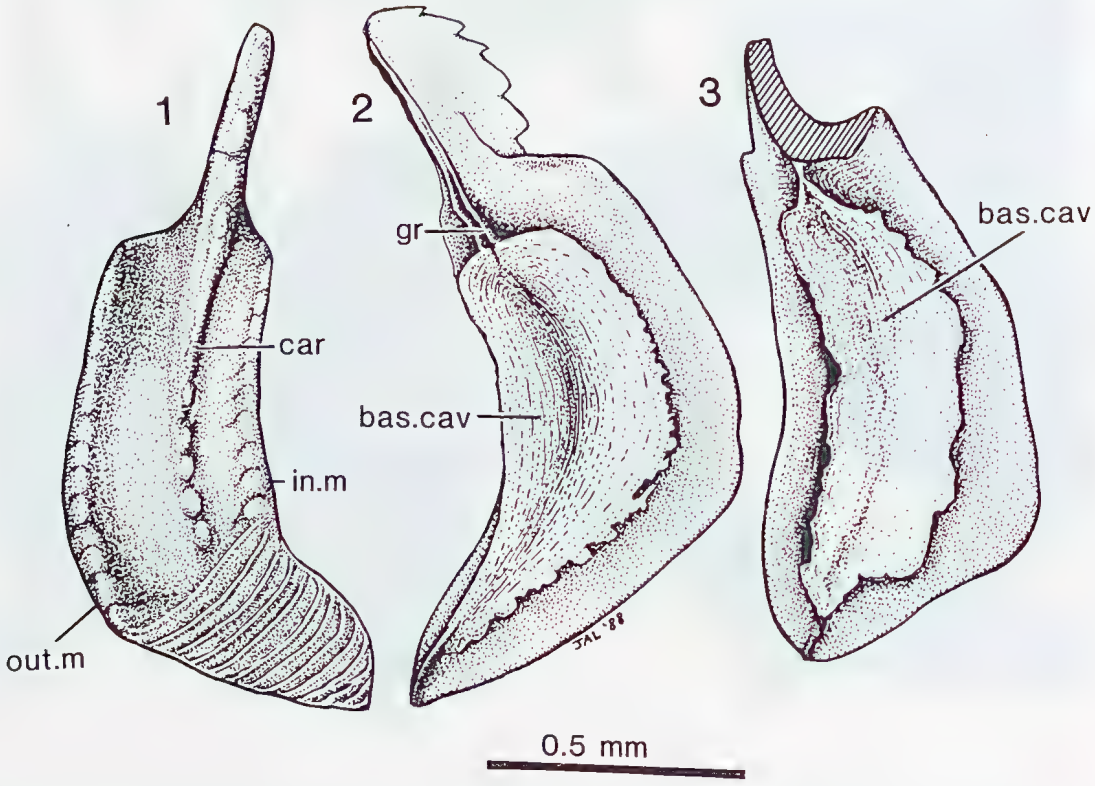

Fig.6. *Polyganthus labiosus mawsonae* n.subsp., large Pa elements. 1, 2, Sketch of holotype UTGD 123642 showing main features, basal cavity partially restored to full shape (note: the anterior region of free blade was present when this sketch was done). 3, basal view of paratype UTGD 123643. bas.cav - basal cavity; car - carina; gr - basal groove; in.m - inner margin; out.m - outer margin.

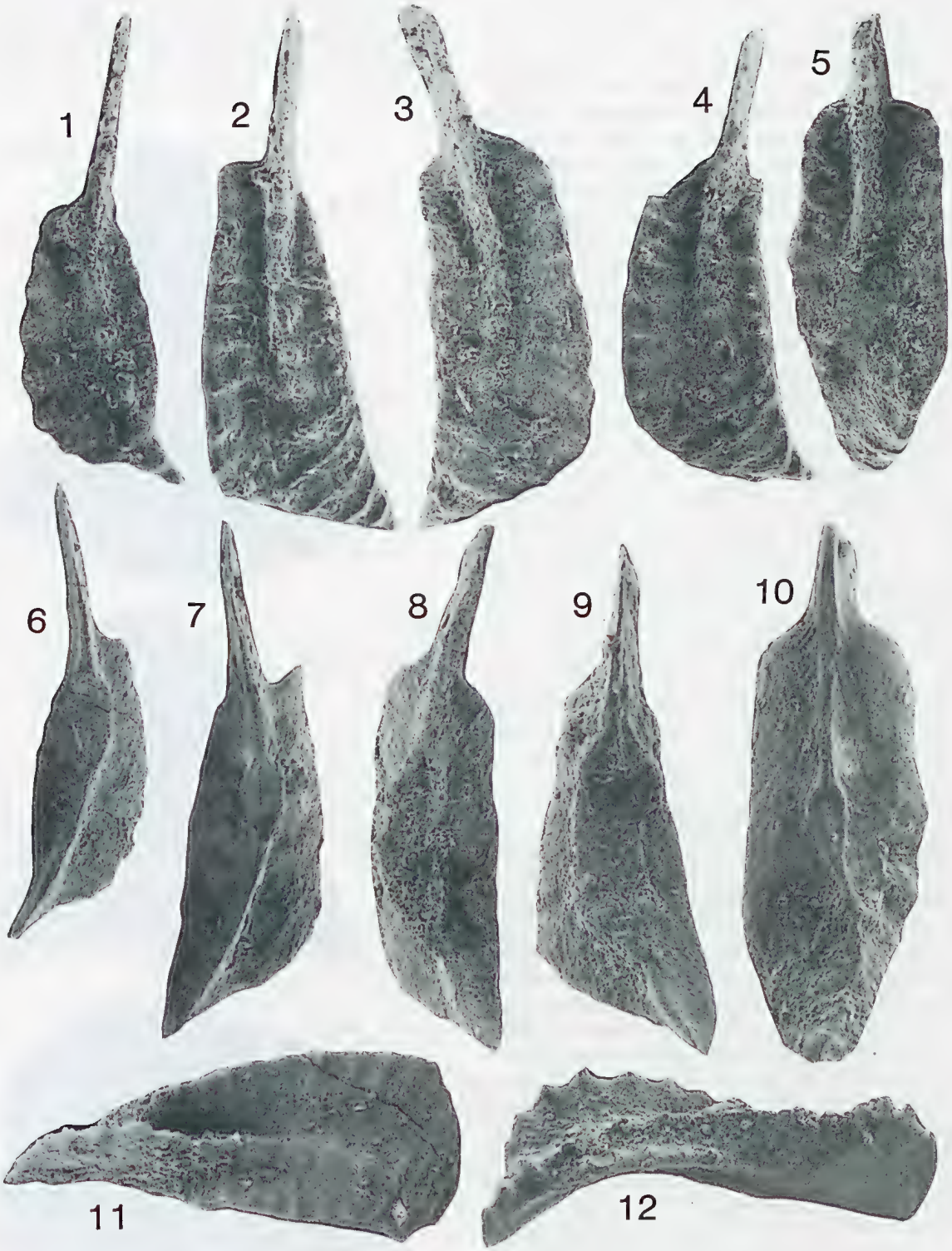

Fig.7. *Polygnathus labiosus mawsonae* n.subsp. Small specimens of Pa elements. 1,2,12, UTGD 123647, x 131; 2, 7, UTGD 123648, x 120; 3, 8, UTGD 123649, x 131; 4, UTGD 123650, x 130; 5, 10, UTGD 123651, x 101; 9, UTGD 123652, x 130; 11, UTGD 123653, x 101.

locality, Buchan, eastern Victoria, in the posterior third of the platform having a broader shape and being considerably broader than the anterior margin of the platform, generally having a larger basal cavity in the biggest elements, and a weaker development of the marginal denticulation. In addition, the anterior margin of the basal cavity is more rounded in the Thai specimens, whereas in *P. labiosus* s.s. the basal cavity tapers anteriorly (Figs 10-12). Most of the Thailand specimens have a strongly deflected platform which has many fine transverse ridges, and only one specimen (Fig. 5.1) has bifurcation of the transverse ridges on the posterior third of the platform. None of the specimens illustrated by Mawson (1987a, pl.35, figs 1-9, pl.36, figs 3,4) show the posterior half of the platform being as broad as the anterior margin, which is the reverse of the case in the Thailand specimens.

The range of variation seen in *P.labiosus mawsonae* n.subsp., is shown in Figures 5, 6, 7 and 10, and ontogenetic variation in the subspecies is discussed below. One specimen (Fig. 5.1, 5.2, 5.6) is particularly broad across the posterior half of the platform and shows an irregular pattern of transverse ridges, some of which are not continuous accross the breadth of the platform. Specimens which appear to have a small basal cavity similar to *P. linguiformis* s.s., but resemble *P. labiosus mawsonae* in all other features have breakage of the flared margins of the basal cavity away from the platform. This was demonstrated by manual dissection of a specimen (UTGD 123671) which displayed a well-preserved basal cavity with flared margins.

Initial examination of our polygnathid Pa elements indicated that perhaps two species were present: a large form with broad flared basal cavity and numerous ridges on the posterior third of the platform, and a smaller form with small basal aperture and fewer ridges on the platform. However, measurements of the platform size versus the basal cavity size indicates that we are dealing with only one species, and the observable differences in form is attributable to either ontogenetic variation or post mortem damage. Juvenile forms show a proportionately smaller basal cavity and the outline of the Pa element is broader and more rounded (Fig. 10). With increased growth the tongue acquires more transverse ridges and projects posteriorly, whilst the marginal denticulation becomes less distinct. The basal cavity develops as a broad posterior expansion of the lips which seam together in the posterior half of the element (Fig. 10.9, 10.10). Large specimens show either good preservation of the broad basal cavity (Fig. 5.6, 5.7, 5.8) or have the lips broken off, leaving a small basal aperture visible (Fig. 5.9, Fig. 7.10). Statistical representation of this phenomenon is shown in Figure 11 which plots the length of the basal cavity/length of the platform versus the platform length, and shows the morphological development of transverse ridges on the platform in parentheses. The bottom line on this graph shows elements in which the flared lips have broken off, whereas the top line represents well-preserved specimens with basal cavity rims intact. Examination of these specimens shows coarse sediment between the flared lips and the aboral surface of the platform (Fig. 5.7).

Such studies have implications to conodont taxonomy. For example, some of our smaller specimens fall within the morphological range of *Polygnathus linguiformis bultyncki* (e.g. Fig. 7.1, 7.2, 7.6, 7.7) or other *P. linguiformis* morphotypes. If growth sequences were not identified we could have assigned these elements to different taxa, and this indicates the need for further studies of growth

Fig.8. *Pseudooneotodus kuantungensis* n.sp. 1, holotype UTGD 123730, x 160; 2, paratype UTGD 123729 x 160; 3, paratype UTGD 123731, basal view, x 160.

sequences in polygnathid taxa to evaluate their taxonomic status. The changes in number of ridges and different development of the carina in *P. linguiformis linguiformis* morphotypes (Ziegler, 1977) would indicate some degree of heterochronic change, such as paedomorphosis (McNamara, 1986), in the evolution of such lineages.

Pseudooneotodus Barrick & Klapper, 1977

***Pseudooneotodus kuangtungensis* n.sp.**

Figs 8, 9

Gen. et sp. indet. A... Philip, 1965: 113, pl.1, figs 1-4.

Etymology. After the Kuan Tung Formation, the type stratum.

Diagnosis. Small (0.3-0.7mm) conoidal elements having an expanded elliptical concave base which is broader than long, tapering to a pointed crown which is separated from the base by a thickened rim. In profile the denticles have gently concave sides.

Material examined. 23 specimens. HOLOTYPE UTGD 123730 (Fig. 8.1). PARATYPES UTGD 123729 (Fig. 8.2), UTGD 123731 (Fig. 8.3). Others UTGD123716-123738 (123735-738 are thin-sections).

Remarks. Philip (1965) described and figured similar elements from the Tyers Limestone, Victoria, but was not sure whether they were conodonts. He referred to other occurrences of these enigmatic cones from the Upper Silurian and Lower Devonian of Europe (Bischoff & Sanneman 1958, Jentzsch 1962). Bischoff & Sanneman (1958) regarded their specimens as detached basal cones of an oistodid conodont, but Philip pointed out that they are composed of a similar substance as the outside surface of conodonts, so cannot be basal cones. Jentzsch tentatively referred the cones to the conodont *Oneotodus* (now *Drepanodus*, Hass 1962) but expressed doubts as to their conodont nature. Uyeno & Mason (1975) described similar cone-like structures which were identified as acodiniform elements of a a new conodont species, *Pelekysgnathus pedderi*. These differ morphologically from *Pseudooneotodus kuantungensis* by their more elongate shape and absence of a well-defined rim marking off the crown from the base, and their occurrence with other elements recognisable as icriodiform. Despite having over 20 elements of this shape, there are no icriodiform elements associated with these in our samples. Thin-sections of our specimens confirm that they are conodonts rather than the dermal denticles of primitive placoderm or elasmobranch fishes. The walls thicken apically and have a multilaminate structure, thus agreeing with the generic diagnosis of Clark *et al.* (1981) - "...stout cones with a deep basal cavity; walls thicken apically, relatively smooth surface". Our elements agree in all respects with this definition, and as they differ morphologically from the two established species, *P. bicornis* and *P. tricornis*, we here erect a new species.

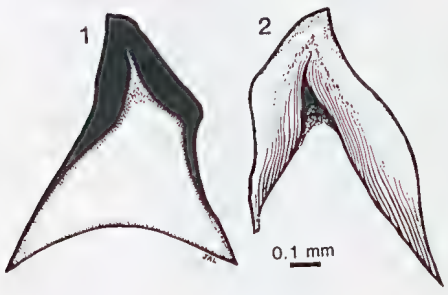

Fig.9. *Pseudoneotodus kuantungensis* n.sp. Sketch of thin-sections of UTGD 123735 (1) and UTGD 123736 (2) showing walls thickening apically and multilaminate structure of apex.

Pseudooneotodus kuantungensis n.sp., which has only one point on the apex, differs from the type species *P. bicornis*, which has two apices, and from *P. tricornis*, which has three apices, mainly by the well defined neck which separates the pointed apex from the stout sides. This feature is clearly visible in the specimens figured by Philip (1965, pl.1, figs 1-4).

It is probable that *P. kuantungensis* (Lochovian-Emsian) is derived from the twin-pointed form *P. bicornis* (Wenlockian), which is probably derived from the stratigraphically younger triple-pointed form, *P. tricornis* (Llandoverian-Wenlockian; Barrick & Klapper 1976; Barrick, 1977).

Biogeographic Implications

Although many conodont species have cosmopolitan distributions, there is a high degree of endemism exhibited by groups of species for specific time periods (Fåhraeus, 1976; Telford, 1979; Charpentier, 1984). Klapper & Johnson (1980) found that the Early Devonian was a time of high endemism for certain conodont species, and this endemism continued until late in the Middle Devonian, when cosmopolitan species start to outnumber the endemic species. Mawson (1987a) revised the taxonomy of certain Early Devonian polygnathids with large basal cavities, and in her review of *P. perbonus* found that most non-Australian occurrences of this species could be referred to her new species, *P. nothoperbonus*. The closely related species *P. perbonus*, *P. labiosus* and *P. pseudoserotinus* are thought to be derived from *P. dehiscens abyssus*, which occur mainly in Australia (Mawson, 1987a). Another new species, *P. pugiunculus* from Queensland, is probably derived from *P. pseudoserotinus* (Mawson, 1987b). The only occurrences of any of these species outside Australia are of *P. perbonus* from the South China Terrane (Wang, 1981, Wang & Ziegler, 1983) and from central Tadzhikstan (Karakum Terrane, Bardashev, 1986), and

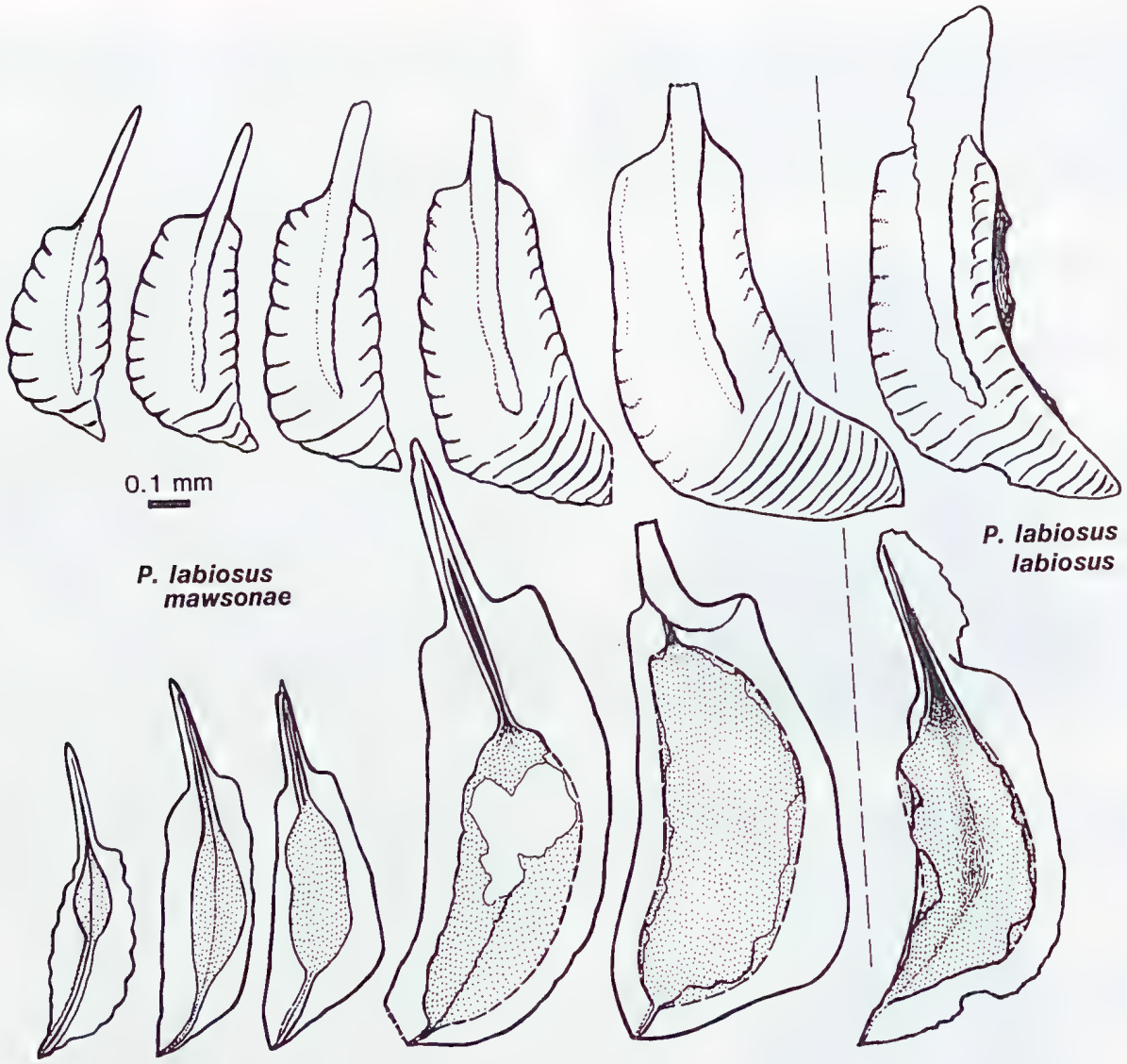

Fig.10. 1-10, ontogenetic variation in *Polygnathus labiosus mawsonae* n.subsp. showing oral and aboral surfaces, basal cavities stippled. 11, 12, an early form of *P. labiosus labiosus* (after Mawson, 1987a: pl.35, figs 1, 2). Note that upper and lower sketches do not correspond to the same specimens (see photos for specimen numbers).

P. pseudoserotinus from Perak, Malaysia by Lane *et al.* (1979; Mawson, 1987a: 277). *Polygnathus declinatus* (Wang, 1979) from the Lower Devonian of South China is either synonymous with *P. pseudoserotinus* or may be a transitional form of *P. inversus* (Mawson, 1987a: 278). *Polygnathus declinatus* would have priority over *P. pseudoserotinus* if there is no 'seaming-up' of the basal cavity. The lineage or clade of polygnathids including *P. dehiscens abyssus* through to *P. pseudoserotinus* most probably originated in the East Gondwana Province, and the only other outside occurrences are from the South China Terrane, the Karakum Terrane (*P. perbonus*; uncertain Devonian palaeoposition), and the Shan-Thai Terrane (*P. pseudoserotinus*). Furthermore, *Pseudooneotodus kuangtungensis* n.sp. is also known only from the Lower Devonian of Thailand and Australia. In a diverse group with generally cosmopolitan distribution, such as polygnathids, the regional restriction of a major clade probably has biogeographic significance. Either these species have not been recognised in other samples, which is highly unlikely given the amount of conodont sampling which has been going on; or alternatively, the group of species in question were restricted to an area encompassing the East Gondwana Province and the Shan-Thai and South China Terranes.

A further test of this hypothesis is to examine the distribution of other groups of taxa showing widespread distribution to see if the pattern of their Early Devonian or later distributions corroborates that of the polygnathids. One such group, the thelodontid agnathans, demonstrates a similar distribution. The species *T. pagoda* (Wang *et al.*,

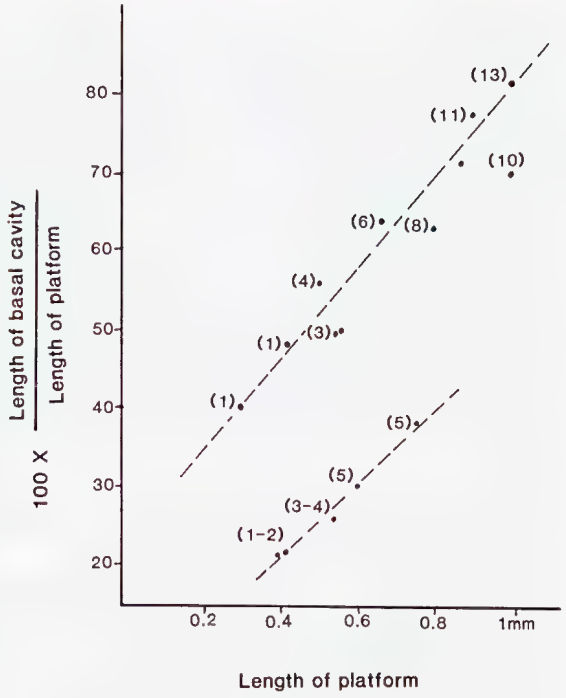

Fig.11. Graphical representation of increasing size of basal cavity with growth for *Polygnathus labiosus mawsonae*. The top line shows specimens preserved with basal cavity complete; the bottom line shows specimens with basal cavity lips broken off, giving the appearance of a smaller basal aperture. Numbers in parentheses refer to number of transverse ridges on the posterior third of the platform. Length of platform measured from ocular of microscope.

1986) occurs in Shidian, west Yunnan (Shan-Thai Terrane, there is good evidence that the Chinese and Shan-Thai Terranes were attached to Gondwana during the Early Palaeozoic (Burrett & Stait 1986, 1987) these Devonian occurrences lead us to suggest that the Shan-Thai Terrane was still in close contact with the eastern margin of Gondwana during the Early and Middle Devonian, as proposed by Bunopas (1981). The South China Terrane was close to these Terranes, and remained so until at least the end of the Devonian as evidenced by the distributions of Late Devonian terrestrial fish, e.g. sinolepids in the Late Devonian of Australia (Hunter Siltstone, NSW), South China and Ningxia (Young, 1987; Pan Jiang, 1987). Further Late Devonian evidence of proximity between the Shan-Thai, East Gondwana and South China Terranes comes from recent new finds of microvertebrates from Northern Thailand. This fauna contains similar species of the chondrichthyan *Phoebodus* from Queensland, Thailand and South China, as well as a peculiar new shark genus only known from South China and Thailand (Long, in press). Figure 12 shows the distribution of endemic polygnathids with large basal cavities on a modified Devonian base map in which the Shan-Thai, North and South China Terranes are located within the palaeolatitudinal controls indicated by Heckel & Witzke (1979), but placed closer to the eastern margin of East Gondwana, as suggested by faunal comparisons. Further descriptions of Shan-Thai Devonian faunas are needed to refine this model and delineate the relationships between East Gondwana, Shan-Thai and the Chinese Terranes (North and South China, Tarim, Quaidam etc.) for stages in the Devonian.

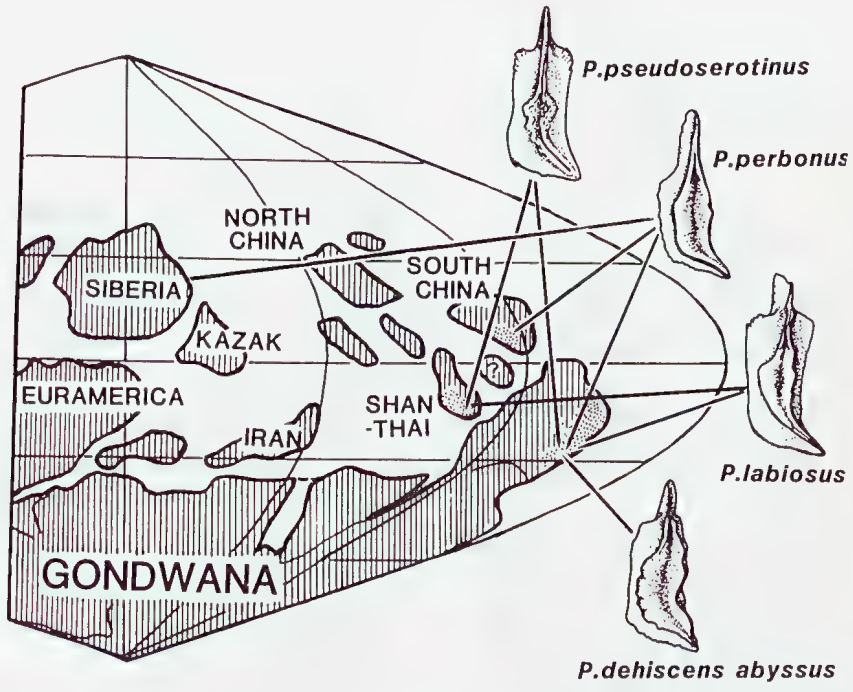

Fig.12. Distribution of certain endemic polygnathid species shown on a modified palaeogeographic base map for the Devonian (after Heckel & Witzke, 1979). Placement of South China, North China, Shan-Thai Terranes is closer to East Gondwana than for previous reconstructions, based on faunal comparisons discussed in text. The small terrane with a question mark between Shan-Thai and South China is the Indo-China Terrane. Polygnathid sketches after Mawson (1987a).

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Synopsis of the Whalefishes (Family Cetomimidae) with Descriptions of Four New Genera

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ABSTRACT. This study of more than 500 specimens recognises two cetomimid subfamilies (one newly described), nine genera (four newly described) and about 35 species (four newly described). Characters of the gill arches, head laterosensory canals, lateral line scales, cavernous tissue, anal lappets and subpectoral organ (the last three of unknown function) are used to distinguish taxa. A cladistic analysis of 39 characters utilised *Rondeletia* and *Barbourisia* as outgroups to polarise character states within the family and the beryciform families to polarise family characters. Three synapomorphies, the presence of gill rakers in some form other than elongate and flattened and the absence of pelvic fins and pleural ribs, support the monophyly of the family. The monotypic Procetichthyinae, defined by four autapomorphies, is the primitive sister group of all other cetomimids. It retains such pleisiomorphic features as a fully developed nasal organ, a fully developed eye with lens, a pseudobranch and 19 principal caudal rays. *Ditropichthys* is the primitive sister group of the remaining seven genera, with the next line including the related *Cetichthys* and *Notocetichthys*. The relationships of the remaining five genera are equivocal, except that *Cetomimus* and *Gyrinomimus* are sister taxa defined by lateral line scale shape. A working hypothesis of relationships is presented that places *Danacetichthys* and *Cetostoma* as sister groups of the remaining three genera. Multistate characters of gill raker-tooth plate shape and extent of the fourth gill slit support the hypothesis. *Cetostoma* and *Rhamphocetichthys* are highly derivative forms, with each monotypic genus defined by three or four autapomorphies. The genera *Gyrinomimus* and *Cetomimus* each have more than ten species, which will be reviewed in later papers. The other genera each have one or two species that are fully detailed here. All examined specimens with recognisable gonads are females, confirmed by histology of eight specimens representing four genera. Egg sizes of at least 2.0, 1.3 and 0.6 mm diameter are attained by the genera *Procetichthys*, *Gyrinomimus* and *Cetostoma* respectively. The vast majority of examined specimens had eggs 0.1 mm diameter or less. The few specimens with larger eggs had bimodal egg sizes. Males and individuals less than 25 mm are unknown. Maximum size is at least 390 mm in one species of *Gyrinomimus*, while *Ditropichthys* and *Cetostoma* apparently do not exceed 140 mm and 250 mm, respectively. Crustaceans are the primary food of whalefishes. The family is distributed in all oceans, from 52°N to 72°S. At the species level, two distribution patterns are apparent. The two commonest species, *Cetostoma regani* and *Ditropichthys storeri*, have cosmopolitan distributions between 50°N and 40°S. The two most frequently captured species of *Gyrinomimus* are restricted to the north Pacific between 39° and 52°N and circumglobally in the Southern Ocean between 32° and 72°S. There are too few collections of the other species to ascertain distributional limits, but some have been taken in all three oceans and others only in a part of one ocean. The centres

of vertical distribution for all species are below 1000 m. Only smaller specimens of *C. regani* and *D. storeri* have been taken above 1000 m, where some nocturnal vertical migration is indicated. Closing net captures confirm large specimens of both species live between 1200 and 1500 m. Four separate closing net captures of *Cetichthys parini* between 2700 and 3200 m demonstrate this to be the deepest living known whalefish. At least some cetomimids are more abundant than previously thought, with 55% of the ISH midwater trawls in the Atlantic fishing to 1800 m or deeper catching whalefishes. Up to 11 specimens and six different species of whalefishes were taken in a single deep trawl. With about 35 species, cetomimids are second only to the anglerfish family Oneirodidae as the most speciose bathypelagic fish family and may be the most abundant below 1800 m. As four of the eight species considered in this paper are represented by less than five specimens, it seems probable that additional species of cetomimids will be captured.

PAXTON, J.R., 1989. Synopsis of the whalefishes (family Cetomimidae) with descriptions of four new genera. Records of the Australian Museum 41(2): 135-206.

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Whalefishes of the family Cetomimidae inhabit the meso- and bathypelagic waters of all oceans. Although 18 species have been described since 1895 (Table 1), the cetomimids remain one of the most poorly known fish families, with fewer than 100 specimens recorded in the literature. Parr (1934) and Harry (1952) summarised what was known of the family. Since 1952 nine additional species have been described, but little synthetic work has been done; Maul (1969) included a key to the known species of *Cetomimus*.

All but two species in the family were originally described from a single specimen and few additional specimens have been described in detail. Characters such as the numbers of fin rays, lateral line pores and rows of teeth in the jaws and vomer have been used to diagnose new species, but the range of variation within a single species has not been recorded, due until relatively recently to the paucity of specimens in collections. Most of the described specimens have been less than 100 mm standard length (SL); the largest specimen recorded to date was 174 mm. As many species exceed 200 mm SL and the largest specimen collected is 390 mm SL, it appears that most previous descriptions have been based on juveniles. Little information has been published concerning whalefish biology and no data are available on reproduction or food. With all previously recorded specimens caught in open nets, the vertical distribution of the family has not been detailed. However most were caught with nets fishing at least to 1000 metres, and the family has long been considered bathypelagic.

The systematic placement of the Cetomimidae has been the subject of controversy. Parr (1929), on the basis of osteological features, included the family within the order Iniomi (= Myctophiformes *sensu lato*), while removing the family Rondeletiidae to the order Xenoberyces (= Stephanoberyciformes). Parr (1945, 1946) and Myers (1946) indicated the Cetomimidae and Barbourisiidae were closely related, but disagreed as to whether the latter should be recognised at the familial or subfamilial level. All subsequent authors have considered all three families closely related, differing in their ordinal placements: as a separate suborder of Myctophiformes (Harry, 1952); as a distinct order Cetomimiformes with or without other families included (Greenwood *et al.*, 1966; McAllister, 1968; Gosline, 1971; Ebeling & Weed, 1973); in the order Beryciformes (Rosen & Patterson, 1969) or with other families in a "stephanoberycoid group" (Rosen, 1973).

A complete family monograph is obviously required. Problems to be solved include those at the alpha taxonomic level (determination of the genera and species represented by the more than 500 currently available specimens), determination of evolutionary relationships at both the generic and familial levels and description of the biology of the whalefishes based on examination of gonads and stomach contents. The present paper summarises knowledge of the family at the generic level based on examination of most of the available specimens, describes four new genera and four new species, defines the other five genera in the family and presents an analysis of generic relationships based mostly on external characters.

Table 1. Nominal taxa of the family Cetomimidae, including new taxa described herein; synonyms are placed in brackets.

Subfamily Procetichthyinae n.subfam.
Procetichthys n.gen.
Procetichthys kreffti n.sp.
Subfamily Cetomiminae Goode & Bean, 1895
(Subfamily Ditropichthyinae Parr, 1934)
Ditropichthys Parr, 1934
Ditropichthys storeri (Goode & Bean, 1895)
Cetichthys n.gen.
Cetichthys indagator (Rofen, 1959)
Cetichthys parini n.sp.
Notocetichthys Balushkin, Fedorov & Paxton, 1989
Notocetichthys trunovi Balushkin, Fedorov & Paxton, 1989
Danacetichthys n.gen.
Danacetichthys galathenus n.sp.
Cetostoma Zugmayer, 1914
Cetostoma regani Zugmayer, 1914
Gyrinomimus Parr, 1934
Gyrinomimus myersi Parr, 1934
(*Gyrinomimus parri* Bigelow, 1961)
Gyrinomimus simplex Parr, 1945
Gyrinomimus bruuni Rofen, 1959
Gyrinomimus grahami Richardson & Garrick, 1964
(*Gyrinomimus notius* Fedorov & Balushkin, 1983)
Gyrinomimus andriashevi Fedorov, Balushkin & Trunov, 1987
Cetomimus Goode & Bean, 1895
(*Pelecinomimus* Gilchrist, 1922)
(*Cetomimus* (*Psapharocetus*) Harry, 1952)
Cetomimus gilli Goode & Bean, 1895
Cetomimus picklei (Gilchrist, 1922)
Cetomimus kerdops Parr, 1934
Cetomimus craneae Harry, 1952
Cetomimus teevani Harry, 1952
Cetomimus compunctus Abe, Marumo & Kawaguchi, 1965
Cetomimus hempeli Maul, 1969
Rhamphocetichthys n.gen.
Rhamphocetichthys savagei n.sp.

Vitiazella Rass (1955) and *Cetomimoides* Koefoed (1955), originally described in the family Cetomimidae, have since been placed in the family Megalomycteridae (Myers & Friehofer, 1966).

Future papers will revise the species within the genera *Gyrinomimus* (about 12 species) and *Cetomimus* (perhaps 15 species), describe the osteology of the genera and analyse family relationships.

Materials and Methods

More than 500 specimens from 25 institutions were examined during the course of the study (Table 2). Most specimens of *Cetomimus* were only cursorily examined for identification to genus, while all others were examined in detail. Museum abbreviations follow Leviton *et al.* (1985). Unless otherwise indicated, all lengths are standard lengths (SL).

Descriptions follow the format of Harry (1952). Vertebral counts and confirmation of questionable fin counts were made from x-rays. Methods of counting and measuring follow Hubbs & Lagler (1949), except that the last dorsal and anal fin element was included in the count (the last ray was sometimes single and sometimes double, see next section). Measurements were made with dial calipers to the nearest 0.1 mm; measurements less than 50 mm were usually made under a dissecting microscope.

In the materials examined sections of each species, only one latitude and longitude are given for each collection. For most stations, this is the midpoint of the trawl; however for some collections (like ISH), it is the start of the trawl. Most whalefishes were caught with open nets and the depth given is from the surface to the maximum depth fished. If no depth gauge was available, the approximate deepest fishing depth for the amount of wire out is given (e.g. 0-ca.2000 m). For a few collections, notably those of the *Discovery*, Oregon State University, Tokai Fisheries and recently of Scripps Institution of Oceanography, closing nets were used and these are indicated. When available the time of day has been converted to an indication of hours of daylight (D) or darkness (N); consideration was given to both latitude and time of year in making the conversions.

Drawings of lateral line scales and anal lappet scales were made with the aid of a dissection microscope and camera lucida. A section of lateral line containing at least two lateral line scales was dissected out of at least one specimen of each genus and stained with alizarin.

The following specimens were measured and/or examined for characters in the outgroup analysis:

Barbourisiidae
Barbourisia rufa
AMS I.26869-001, 89.5 mm, Zanzibar
AMS I.27260-001, 91.7 mm, Hawaii
AMS I.18824-001, 100 mm, Hawaii, cleared and stained (C+S)
AMS I.22812-002, 110.9 mm, northwest Australia
AMS I.27261-001, 133 mm, central Pacific (C+S)
MCZ 49148, 165.8 mm, Hawaii
CSIRO H1150-01, 305 mm, Tasmania
Rondeletiidae
Rondeletia bicolor
AMS I.18415-001, 59.9 mm, north Atlantic

Rondeletia loricata
AMS I.20306-005, 44.7 mm, southeast Australia
AMS I.21368-005, 44.7 mm, southeast Australia
AMS I.20307-011, 60.7 mm, southeast Australia
AMS I.24859-001, 76.1 mm, southeast Australia
LACM 9571-5, 77.5 mm, southern California
LACM 9254-33, 94 mm, southern California (C+S)

Diagnostic Characters

Previous descriptive studies on cetomimids have utilised primarily meristics, morphometrics, dentition, the shape of lateral line pores and the location of cavernous tissue to distinguish taxa. Description of these and other characters of the eye, nasal organ, lateral line system and gill arches are given here.

Meristic characters. Counts useful in distinguishing taxa include dorsal, anal, pectoral and caudal fin rays, vertebrae and lateral line pores and scales. Pelvic fins are absent and branchiostegal rays were counted only in a few cleared and stained specimens.

The first four or five dorsal and anal rays are often much shorter than the remaining rays, and in some genera embedded in tissue with only the tips of the first two or three rays exposed and often associated with cavernous tissue. Dissection or x-rays are sometimes necessary to confirm these counts. The last ray of the dorsal and anal fin is almost always single and much smaller than the penultimate ray. In cleared and stained specimens of *Cetostoma regani*, *Ditropichthys storeri* and *Gyrinomimus grahami*, the last anal ray has its own separate radial while the last dorsal ray shares the radial of the penultimate ray. Not enough specimens have been cleared and stained to determine if the radial/ray relationship is consistently different in the two fins throughout the family. All rays of each fin have been counted in this study and the cetomimid counts represent fin rays, not necessarily radials. However the last two rays are counted as one in the outgroup families considered in the last section, as *Rondeletia* and *Barbourisia* have the last two rays of each fin on a single radial. The tips of the dorsal, anal and caudal fins are usually lost due to abrasion in the net; usually no distinction has been made between simple and branched rays, because this may be artificial, depending on how much of the distal portions of the branched rays has been lost.

Similarly recognition of principal caudal fin rays was often subjective when the ends of the rays were lost; unlike some other fishes such as myctophids (Paxton, 1972), the rays immediately outside the branched rays, the first and last principal rays, are not greatly enlarged relative to the series of procurrent caudal rays, in all genera except *Cetostoma*. The principal rays could only be counted with assurance when some of the branched portions of each ray were present. The number of procurrent caudal rays could only be determined on cleared and stained specimens or on those with badly torn skin; dissections were not made on other specimens.

The pectoral fins in all cetomimids except *Procetichthys* are small and have 17 to 24 rays. In most genera the ventral-most six to eight rays decrease in size and are often difficult to count in small specimens, even with dissection. It was often necessary to dissect the thick skin over the

Table 2. Specimens by genus and collection.

Inst.	*Procetichthys*	*Ditropichthys*	*Cetichthys*	*Notocetichthys*	*Danacetichthys*	*Cetostoma*	*Gyrinomimus*	*Cetomimus*	*Rhamphocetichthys*	Totals
ISH	1	24	1		1	55	39	22	1	144
SIO		13	2		1	14	18	39		87
LACM		12	1			8	19	26	1	67
IOS		4				27	1	12		44
ZIN		5	2	2		5	18	8		40
ZMUC		3	1		2	7	4	16		33
MCZ		7				7	3	12	1	30
AMS		6	1			3	7	11	1	29
USNM		2			1	4	3	9		19
OSUO		1	2			7	9	1		20
TH		3					2	8		13
UMML		2				6		5		13
BOC		1				3	2	1		7
CAS		1				2	1	2		6
ORI								3		3
NSMT			2		1					3
MMF								3		3
ORSTOM							1	1		2
BCPM							1			1
FAKU								1		1
HUMZ						1				1
MOM						1				1
NMNZ							1			1
RUSI								1		1
Totals	1	84	12	2	6	150	129	181	4	569

pectoral base to count the rays.

The distinction between precaudal and caudal vertebrae was not clear on the x-rays and every count involved some degree of subjectivity. In cleared and stained specimens of *Cetostoma regani* and *Ditropichthys storeri* fused neural and haemal spines were only present posterior to the dorsal and anal fins, while in a cleared and stained *Gyrinomimus grahami* the haemal arch under the second anal pterygiophore was closed and the next 11 arches were open. Therefore the vertebral count was divided arbitrarily into preanal and anal vertebrae, with the first anal vertebra defined as that directly over the internal end of the first anal pterygiophore. The caudal complex, including the first preural and ural centra, was counted as the last single anal vertebra. Although the second preural vertebra, immediately before the caudal complex, usually carries double neural and haemal spines indicating fusion (see Rosen, 1973: figs 54, 55), these were counted as a single vertebra if only one centrum was apparent. The first vertebra is incomplete, lacking the broad anterior face typical of other centra where it articulates with the skull; it can usually be distinguished on x-rays by the presence of a neural spine.

In the gill raker or gill tooth plate counts the element in the angle of the arch is included in the count of the ventral arm, and all rudiments, even the smallest tooth plates, are included in the dorsal and ventral arm counts. In the tooth plate counts of the gill arches of *Cetostoma*, the individual tooth plates are recognisable and counted as separate even in the largest specimens where some fusion has begun. In contrast, plates are counted as one when partial fusion has begun in *Gyrinomimus* and *Cetomimus* where fusion eventually obliterates the original margins.

The lateral line pore count begins at the top of the gill slit and includes the last pore on the caudal fin base. More details are discussed in the section on the lateral line system.

Morphometric characters. A total of 20 body proportions was measured for each species and analysed as percentages of standard length. Although all measurements were made to 0.1 mm, and some critical measurements of distorted specimens were made on both sides and averaged, the accuracy of all but the smallest measurements is closer to 1 mm than 0.1 mm, due to the flabby nature and damaged condition of most specimens. For the new species in the four new genera, all specimens were measured. For the monotypic genera *Ditropichthys* and *Cetostoma*, at least 20 specimens of each were measured and analysed for allometric growth. For the genus *Cetomimus* 15 specimens representing at least six species were measured. The ranges of measurements for *Gyrinomimus* include data on 60 specimens representing eight species.

Shrinkage of fishes in preservative is well known and seems to affect cetomimids more than many others. No specimens were measured freshly caught, but numerous specimens were measured twice, at least for standard length, over a number of years and considerable shrinkage noted. A specimen of *Gyrinomimus grahami* was measured within six months of original preservation in 1964 and again 22 years later; the standard lengths were 227.5 mm and 202.8 mm, involving a shrinkage of 10.9%. It is possible that differential shrinkage occurs, with those proportions supported by bone (i.e. standard length) shrinking at a different rate than those not supported by bone (i.e. body depth) (S.H. Weitzman, personal communication, 2 Aug. 1988). In the absence of a detailed study over time, it is here assumed that all parts shrink proportionally and that ratios are not adversely affected provided all measurements are made in the same year.

The methods of measurement follow Hubbs & Lagler (1958), with the following exceptions or elaborations: lower jaw length (LJL) - from the anterior tip of the dentary to the posterior tip of the lateral spine of the lower jaw; posterior premaxilla to opercular margin (Pm-Op) - from the posterior tip of the upper jaw to the opercular margin at the level of the pectoral fin; eye width (EW) - from the centre of each eye; head width (HW) - from the bony projections of the sphenotics anterodorsal to each eye; postpremaxillary width (PmW) - from the posterior tip of each premaxillary; body depth (BD) - at the level of the pectoral base; anus to anal origin (An-AO) - from the centre of the anus to the base of the first anal ray.

Other abbreviations used in the tables are as follows: SL - standard length; HL - head length; SnL - snout length; PmL - premaxillary length; ED - eye diameter; D-A - dorsal origin to anal origin; CPD - caudal peduncle depth; CPL - caudal peduncle length; Sn-P - snout to pectoral base; PL - pectoral length; Sn-D - snout to dorsal origin; DB - dorsal base length; Sn-A - snout to anal origin; AB - anal base length; CopL - copular tooth plate length; CopL/W - copular tooth plate length to width ratio; D - dorsal fin; A -anal fin; P - pectoral fin; C - caudal fin; Vert. - vertebrae; LLSc - lateral line scales; GR - gill rakers or tooth plates.

Eye morphology. A number of authors have remarked on the small size of the eye in cetomimids, but few have studied the morphology in detail. Brauer (1908) described the eye of *Cetomimus gilli* (*C.* sp. *fide* Parr, 1928:176) based on microscopic sections. Harry (1952) stated that *Ditropichthys* had no eyes and only the optic nerve branches were present in the pigmented areas. Munk (1965) summarised the information on cetomimid eyes, described the eyes of *Gyrinomimus* and *Ditropichthys storeri* based on microscopic sections and showed that Harry's interpretation of the eye in *Ditropichthys* was erroneous. All of the three cetomimids studied had small, degenerate eyes. Brauer's (1908) *Cetomimus* had a rudimentary lens which was lacking in the specimens described by Munk (1965). Munk described a number of other degenerate features, including reduced or absent iris and acellular retinal pigment granules associated with the degenerate retina. The eye of *Gyrinomimus* was considered more degenerate than that of *Ditropichthys*, and it was suggested that the eye of this latter genus was probably fully differentiated before degeneration. Munk

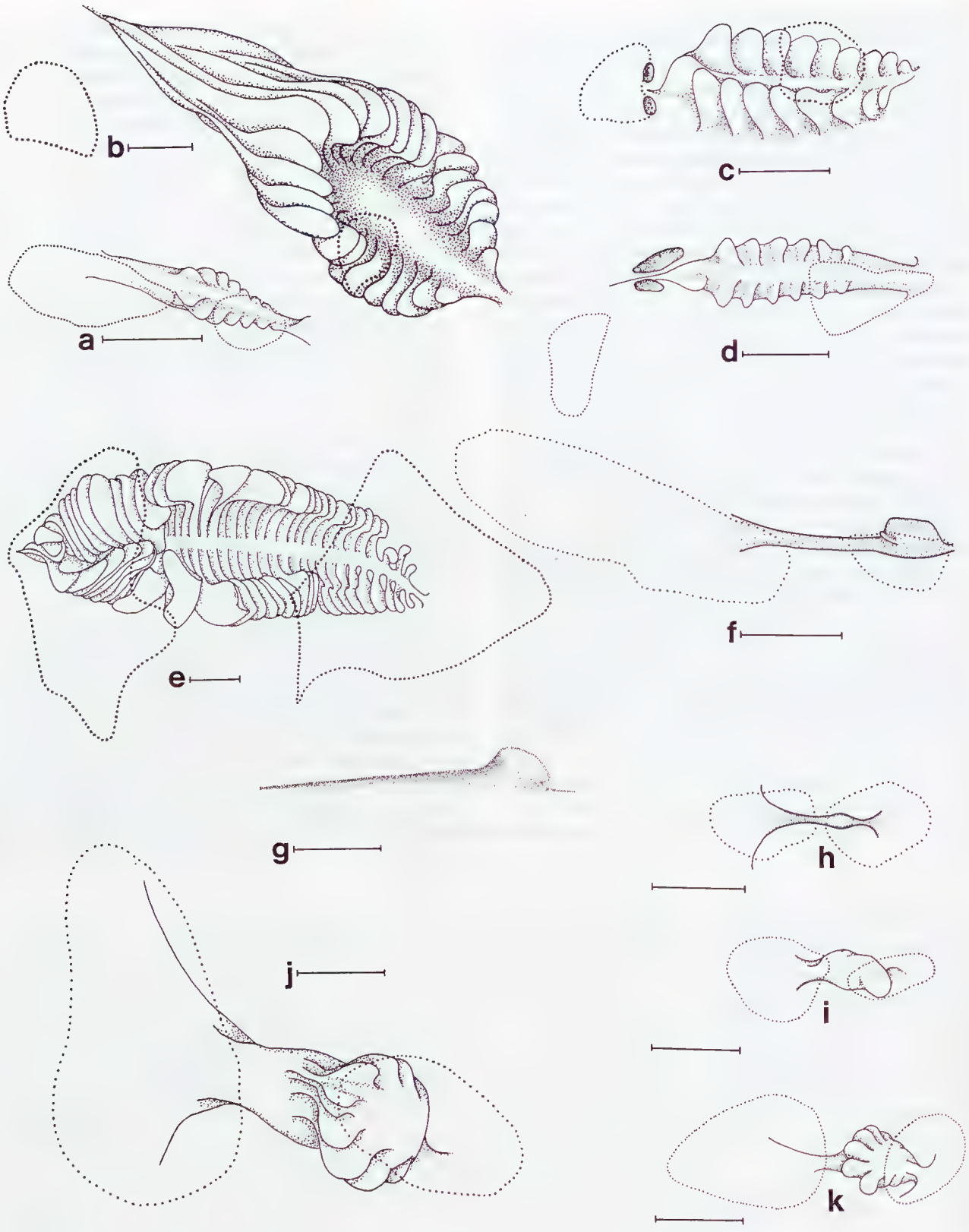

Fig.1. Nasal organs; nostrils shown with dotted lines; right side, anterior to right; scale bars equal 1 mm. a, *Barbourisia rufa*, 91.7 mm, AMS I.27260-001; b, *B. rufa*, 296 mm, ORSTOM New Caledonia; c, *Rondeletia bicolor*, 59.9 mm, AMS I.18415-001; d, *R. loricata*, 82 mm, AMS I.18814-001; e, *Procetichthys kreffti* holotype, 236.5 mm, ISH 1188/71; f, *Ditropichthys storeri*, 84.4 mm, AMS I.18816-001; g, *Cetichthys parini* paratype, 96.0 mm, AMS I.27258-001; h, *Danacetichthys galathenus* paratype, 53.9 mm, NSMT P60002; i, *Rhamphocetichthys savagei*, 110 mm, ISH 2297/71; j, *Gyrinomimus* sp. D, 151.0 mm, AMS I.20314-010; k, *Cetomimus* sp. A, 79 mm, AMS I.20524-001.

(1965:28) concluded that light detection might be possible in the degenerated retinas.

No comparative microscopic sections were attempted in this study. Although Munk (1965:21) warned that ocular degeneration can only be studied seriously by histological methods, some comparative observations are made here. The relative size of the eye is easily measured with calipers under a dissecting microscope, and the horizontal diameter is given in this study as a percentage of standard length. While very small eyes of fishes can be functional (e.g. female ceratioid anglerfishes, Munk, 1965), none of the degenerated eyes described in previous studies were moderate or large in diameter. A second feature that is discernible without histology is the presence of a lens. The two states reported here (lens present or absent) are based on examination under a dissecting microscope.

Nasal organ. In all cetomimids there are two nostrils on each side of the head, located about halfway between the eye and the tip of the snout. The anterior nostril is usually about half the size of the posterior nostril and the skin bridge between the nostrils about half the size of the anterior nostril. In the only specimen of *Procetichthys* the nostrils are much larger than the head pores of the lateral line system and the olfactory epithelium is developed into a large nasal organ consisting of a central raphe and fully developed lamellae on each side, almost filling the nasal cavity (Fig. 1e). In all other cetomimids both nostrils are smaller, about equal in size to the head pores, and the nasal organ is greatly reduced, usually consisting of a raised area of olfactory epithelium, presumably homologous to the central raphe, but without lamellae (Fig. 1f--i). In some species of *Gyrinomimus* and *Cetomimus* a spherical mass of olfactory epithelium arises from a ventral ridge and low, thin lamellae are found around the sphere (Figs 1j,k). Kleerekoper (1969:50) summarised data on the number of lamellae for a variety of species and pointed out that both the number of lamellae and their size increase with age. I amellae were absent in a number of cetomimid taxa that were represented only by juveniles, as indicated by their immature gonads.

Dentition. Three different arrangements of teeth are found in cetomimid jaws. In most genera the teeth are very small and closely set in approximately diagonal rows and are either conical or triangular in shape (Fig. 2b,d-f). In *Gyrinomimus* and *Danacetichthys* the teeth are small and closely set, but are in longitudinal rather than diagonal rows (in all but one species) and are distinctly elongate, with the older teeth more than three times longer than wide at the base (Fig. 2c). The teeth of *Procetichthys* are widely spaced in 1-2 longitudinal rows and while elongate, are distinctly more pointed than those of *Gyrinomimus*, almost approaching canines in shape if not in size (Fig. 2a).

In *Gyrinomimus*, new teeth are added both to the outer edge of the jaws, as additional rows, and at the posterior of the jaws, as additional series of rows. The inner row of teeth is always the longest, indicating continual growth of teeth. In some specimens, these new, shorter teeth are not fully calcified and are soft and flexible under a probe. In a very few specimens of *Gyrinomimus* all of the jaw teeth (and palatal teeth as well) are decalcified, soft and flexible, as if some basic chemical reorganisation were taking place; the condition is not correlated with size or preservation history.

In almost all species, teeth are also found on the vomer, palatine, ectopterygoid, copula, and four gill arches. These teeth, particularly those on the gill arches (Fig. 3), are similar to but smaller than the jaw teeth. All of these bones also add teeth with growth. Previously the number of tooth rows in the jaws and vomer has been used as a diagnostic character, particularly for species of *Gyrinomimus*. However the number of tooth rows increases with size; the number of vomerine tooth rows ranges from two to eight in *G. grahami* from 68 to 282 mm SL (Paxton, ms).

All of the teeth are depressible towards the centre of the

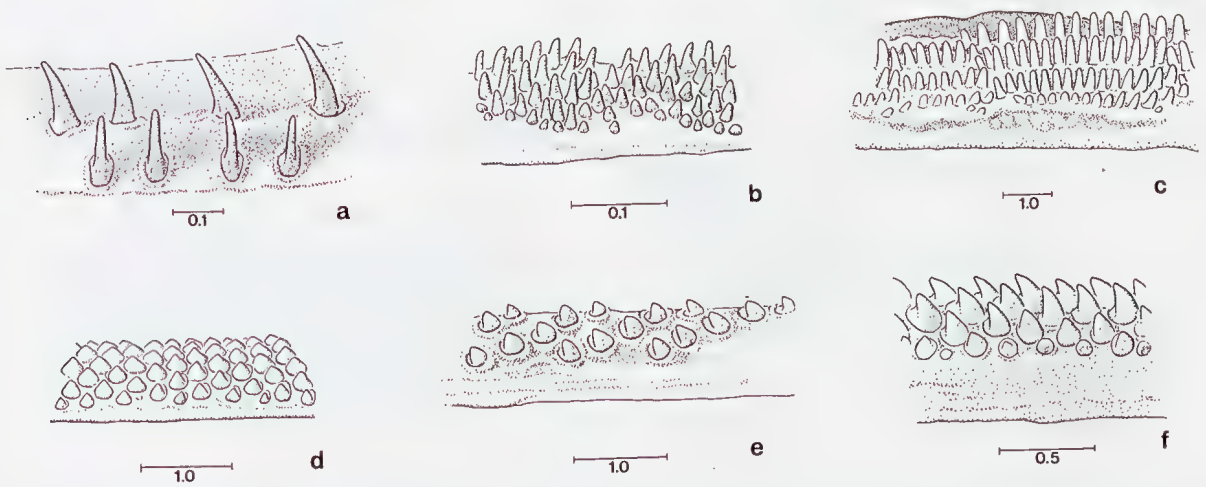

Fig.2. Premaxillary teeth; right side, anterior to right; scale bars in mm; a, *Procetichthys kreffti* holotype, 236.5 mm, ISH 1188/71; b, *Cetichthys parini* paratype, 96.0 mm, AMS I.27258-001; c, *Gyrinomimus* sp. D, 151.0 mm, AMS I.20314-010; d, *Rhamphocetichthys savagei* paratype, 90.8 mm, LACM 30034-11; e, *R. savagei*, 110 mm, ISH 2297/71; f, *Cetomimus* sp. A, 116.7 mm, LACM 11500-1.

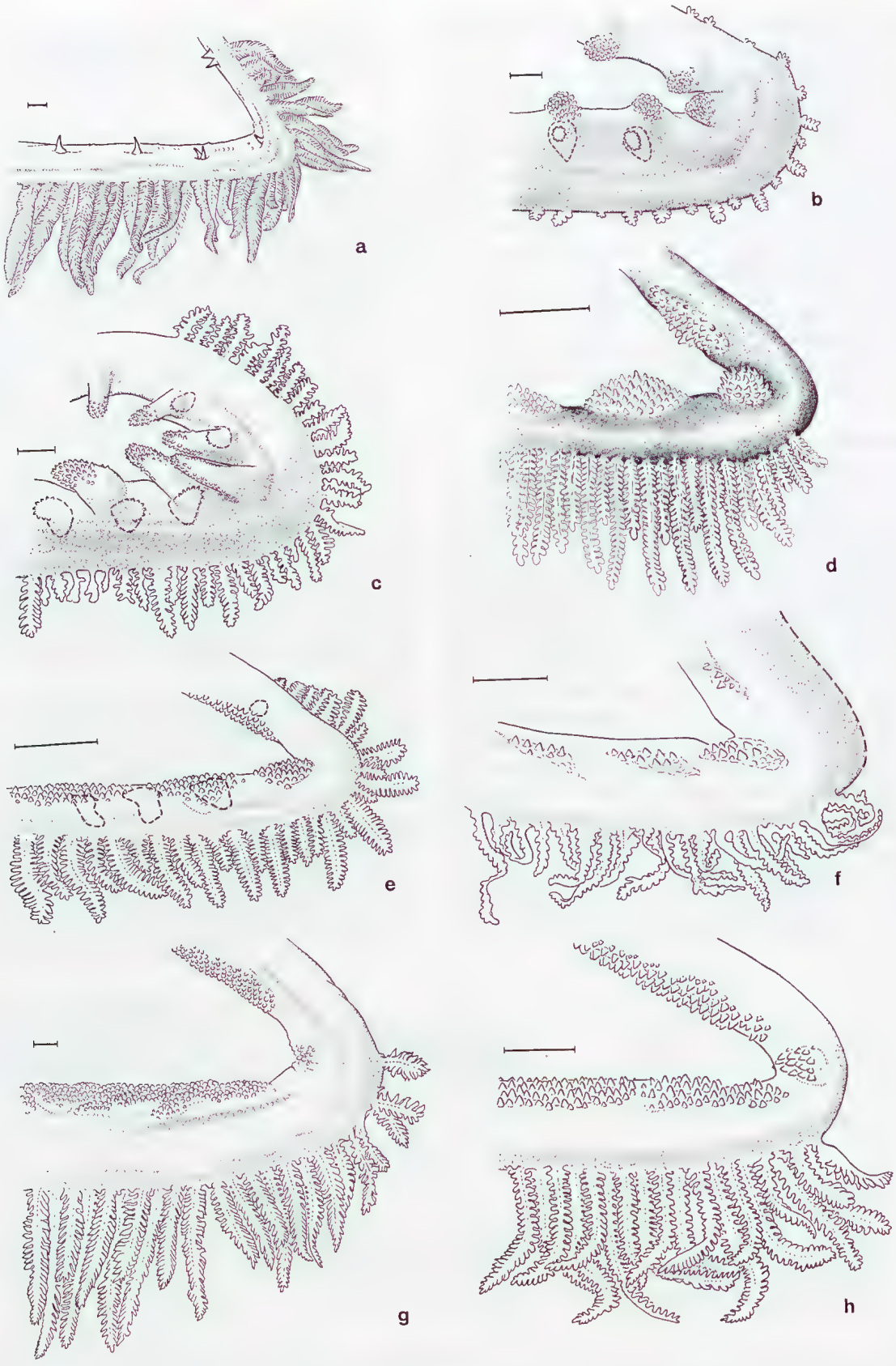

Fig.3. First gill arches; lateral view, left side, anterior to left; medial tooth plates shown with dashed lines; scale bars equal 1 mm; a, *Procetichthys kreffti* holotype, 236.5 mm, ISH 1188/71; b, *Cetichthys parini* paratype, 96.0 mm, AMS I.27258-001; c, *Ditropichthys storeri*, 84.4 mm, AMS I.18816-001; d, *Danacetichthys galathenus* paratype, 53.9 mm, NSMT P60002; e, *Cetostoma regani*, 83.5 mm, ZIN 47884; f, *Rhamphocetichthys savagei* paratype, 90.8 mm, LACM 30034-11; g, *Gyrinomimus* sp. J, 231.3 mm, ZIN 47889; h, *Cetomimus* sp. A, 79 mm, AMS I.20524-001.

oral cavity, except the non-depressible jaw teeth of *Procetichthys*. Fink (1981) has differentiated four types of tooth attachment, with three types involving depressible teeth. In a 141 mm SL cleared and stained specimen of *Gyrinomimus grahami*, there is a large area of unmineralised tissue (presumably collagen) on the oral (posterior/medial) side of the base of each tooth. On the labial (anterior/lateral) side the base meets the underlying jawbone. It is not clear whether there is a thin layer of unmineralised tissue over the labial side of the base, but the hinge appears to involve primarily the tissue on the oral side, indicating a type 4 tooth attachment. The jaw teeth of *Gyrinomimus* can be depressed to an angle approaching 90°. Of the other cleared and stained specimens, only *Cetomimus* has teeth large enough to determine that tooth attachment is also probably type 4.

Gill arches. Elements of five gill arches are present in all cetomimids, with the fifth only visible in a few genera as ventral pharyngeal tooth plates. In most genera, four free gill arches are apparent, with a small to moderate gill slit behind the ventral arm of the fourth arch. The dorsal arm of the fourth and usually the third arches are bound in the skin of the gill chamber. In three genera there is no slit behind the fourth gill arch and only three free arches are present, while in *Cetostoma* the slit is in the form of a small tubular opening behind the angle of the fourth arch.

A range of gill raker types is displayed by the family, from fully developed club-shaped rakers of *Ditropichthys* (Fig. 3c), to the toothed knobs of *Cetichthys* (Fig. 3b) and *Notocetichthys* (Fig. 19c), the individual gill teeth of *Procetichthys* (Fig. 3a) to the tooth plates, either individual or coalesced, of the other genera (Figs 3d-h). Tooth plates are present on the medial face of the first arch in some genera. Gill rakers or tooth plates are present on arch two and three in all genera except *Rhamphocetichthys*.

The shape and extent of the holobranchs are also variable. The two species of *Cetichthys* are extraordinary in having greatly reduced holobranchs (Fig. 3b). The extent of the dorsal arm of the various arches that bears holobranchs is variable. While the holobranchs on the first three arches are fully developed, except in *Cetichthys*, those on the fourth arch are large in some taxa and tiny in others.

There are two pairs of upper pharyngeal tooth plates, associated with the pharyngobranchials of arches three and four. As with the jaw and vomerine teeth, the individual numbers of teeth on the upper pharyngeals, and copula, have been considered important in previous descriptions. However as with the jaws and palate, tooth numbers increase with growth, and individual counts have not been included here. Although the copular tooth plate adds teeth with growth, allometry is uncommon and the relative length differs significantly amongst genera. The size and shape of the copular tooth plate are shown in the individual species drawings (Figs 10, 13, 18, 19, 20, 21, 26, 27, 28). The shape of this tooth plate, expressed as a length/width ratio, differs between species, particularly within *Gyrinomimus*. Functionally the pharyngeals and copular tooth plate do not act as a grinding or crushing organ as they are not directly opposed. Rather food items are apparently moved posteriorly as the copular tooth plate presses against the edentate roof of the mouth behind the vomer and the upper pharyngeals press against the edentate floor of the mouth behind the copula. The lower pharyngeals, when present, are located behind the level of the upper pharyngeals. In contrast to all other genera, *Notocetichthys* has the dorsal pharangeals oriented medially rather than ventrally, so the tooth plates of either side move against each other. Perhaps this is related to the edentate condition of the rest of the palate in this genus.

Lateral line system. The lateral line system is well developed and in all genera, except *Rhamphocetichthys*, consists of a series of wide head canals pierced by large pores in the skin forming the roof of the canals, with receptor organs, the neuromasts, in the floor of the canal between the pores; a large trunk canal is present in all but two genera. The various head canals lie on top of dermal head bones, but the sides and top of the wide canals are formed by skin. The various dermal bones are flat, without raised edges, and do not form the bony troughs typical of many beryciform and stephanoberyciform fishes (see Ebeling & Weed, 1973). The basic pattern of head canals is that typical of teleost fishes, with a continuous canal (supraorbital plus main) extending from the tip of the snout to the top of the gill slit where it becomes the main trunk canal in all genera except *Procetichthys* and *Rhamphocetichthys*, one branch behind and under the eye (infraorbital) and another down the preopercle (preopercular) and along the lower jaw (mandibular). The nomenclature of the various canals follows Coombs *et al.* (1988). The number and arrangement of pores, as well as the connections and cross connections between the main branches, differ between species and genera (Fig. 4). In some species the head is damaged so that connections between canals could not be determined. In *Rhamphocetichthys* no canals or pores are evident; rather, a series of large papillate neuromasts are present and what appear to be nerves, just under the surface of the skin, follow the typical canal pattern (Fig. 4g).

Coombs *et al.* (1988) have summarised the diversity of canal variation in fishes. Their nomenclature for the canals is used here, with some modification. The supraorbital, infraorbital, mandibular and preopercular canals are easily identifiable in cetomimids. However the three portions of the main canal between the juncture of the supraorbital and infraorbital branches and the beginning of the main trunk canal just dorsal to the top of the gill opening are not clear in whalefishes. The three portions, the otic, postotic and temporal canals, are distinguished by their innervation and defined by the junctures of the preopercular and supratemporal canals with the main canal (Coombs *et al.*, 1988, fig. 22.11). In cetomimids, the preopercular canal does not join the main canal, and the distinction between otic and postotic canals cannot be determined externally, while the temporal canal posterior to the supratemporal branch is absent in at least *Cetichthys* (Fig. 4c). Therefore in the following discussion these three portions of the main canal

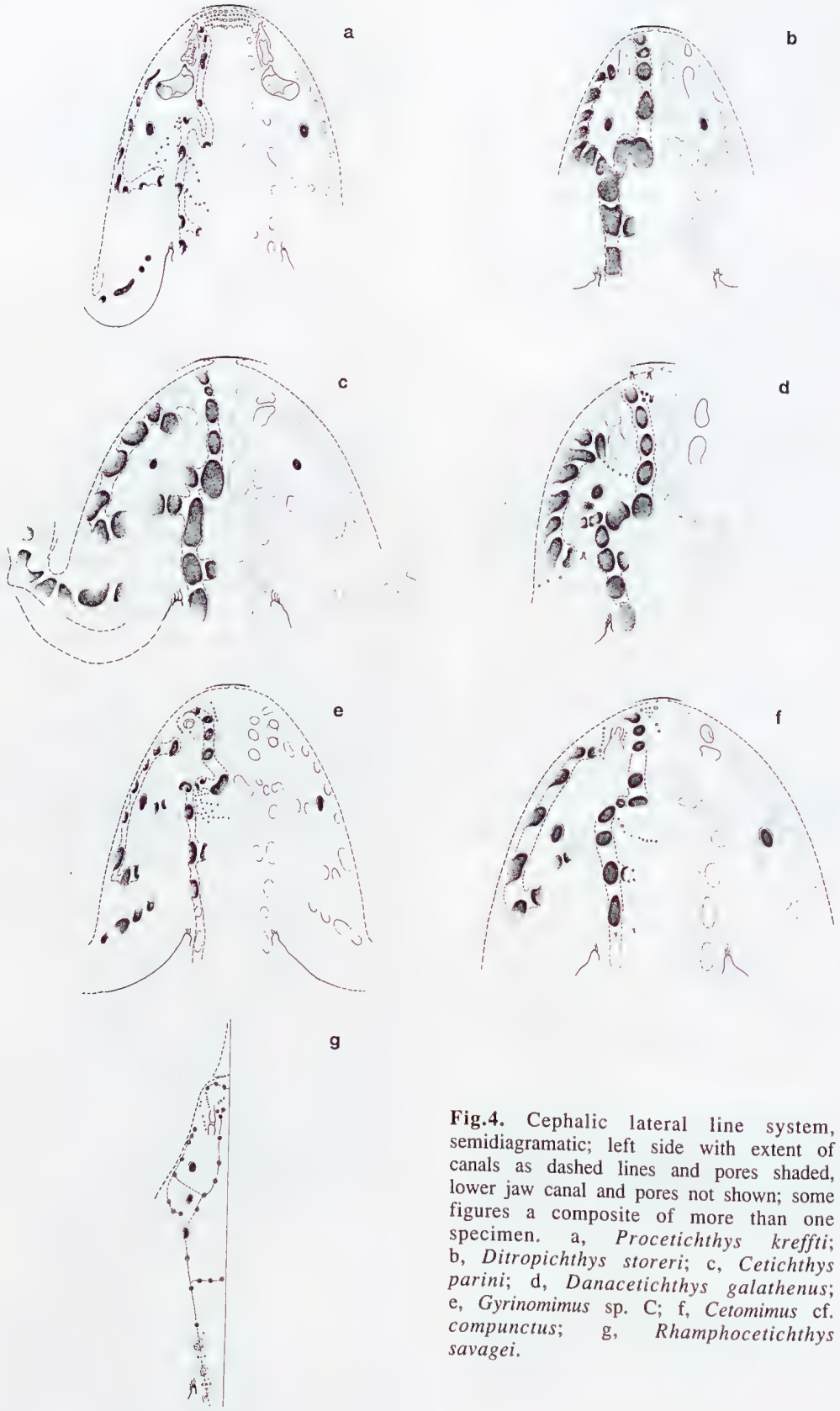

Fig.4. Cephalic lateral line system, semidiagramatic; left side with extent of canals as dashed lines and pores shaded, lower jaw canal and pores not shown; some figures a composite of more than one specimen. a, *Procetichthys kreffti*; b, *Ditropichthys storeri*; c, *Cetichthys parini*; d, *Danacetichthys galathenus*; e, *Gyrinomimus* sp. C; f, *Cetomimus* cf. *compunctus*; g, *Rhamphocetichthys savagei*.

are not distinguished. Because the infraorbital canal does not join the supraorbital canal in all cetomimid genera, the division between supraorbital and main canals is occasionally subjective. In *Cetostoma*, *Gyrinomimus* and *Cetomimus* the supraorbital canal (with six to seven pores) is not joined to the main head canal (Fig. 4e,f).

The supraorbital canal runs from the tip of the snout, anteromedial to the anterior nostril, along the dorsal midline to the fifth pore (the coronal pore of Fedorov & Balushkin, 1983:741), then curves laterally about the level of the eye for one or two pores. The first two supraorbital pores are usually smaller than average and the fifth pore is the largest of the series. The fifth pore is separated from that on the other side of the dorsal midline by a narrow or wide strip of skin. In those genera with the largest head canal pores (*Ditropichthys*, *Cetichthys*, *Danacetichthys* and presumably *Notocetichthys*), the infraorbital canal joins the supraorbital canal at or just behind the lateral curve of that canal, thus restricting the supraorbital to six pores (Fig. 4b-d). In *Procetichthys*, the infraorbital approaches the supraorbital further posterior (Fig. 4a).

The main canal includes two to five pores, with a single pore, representing the supratemporal branch, lying medial to the second or third pore of the main canal. The short supratemporal branch does not reach the dorsal midline in any cetomimid. The total number of pores in the combined supraorbital and main canals ranges from eight to 12.

The infraorbital canal has seven to ten pores, with the first posterolateral to the nostrils. The next four to five pores are under the eye just above the upper jaw, before the canal turns dorsal and somewhat anterior behind the eye. Only in *Cetichthys* is the infraorbital canal continuous with the main canal; these are joined at main canal pore 1 with a small but distinct skin bridge over infraorbital neuromast 8. In *Ditropichthys* there is no remnant of a skin bridge in any specimen, although there is a neuromast between infraorbital pore 8 and main canal pore 1. In all other genera the canals are separate or the condition is unknown. In *Gyrinomimus* and *Cetomimus* the last infraorbital neuromast is usually displaced dorsally and/or anteriorly so the last segment of the canal is separate and either the seventh or eighth pore has two parts that appear as separate, half moon-shaped pores; however these are counted as a single pore so there is always one more pore than neuromast in the infraorbital series (except for *Cetichthys* and *Ditropichthys* where a neuromast follows the last pore, and *Procetichthys* where a neuromast precedes the first pore). Even in the genera with infraorbital canals joining or approaching the main canal, there is a considerable distance between the last two infraorbital neuromasts and the third before the end, but not in *Cetostoma* where the last organ is close to and directly above the penultimate neuromast of the infraorbital series.

The mandibular canal runs along the ventral sheet of the dentary and articular and has five to eleven pores (more than eight only in some species of *Gyrinomimus* and *Cetomimus*) and four to ten neuromasts. The last pore is located just anterior to the ventral spine at the posterior end of the lower jaw. In all but three genera the mandibular canal is separate from the preopercular canal. In *Notocetichthys*, *Gyrinomimus* and *Cetomimus* the two canals are joined, with a neuromast between the two adjacent pores. The first, ventralmost preopercular pore is defined as the one immediately posterior to a line joining the lateral and ventral spines of the lower jaw. The preopercular canal begins just behind the posterior edge of the lower jaw and runs dorsally behind the posterior tip of the premaxilla, usually to the level of the eye; the preopercular canal does not join the main canal in any species of cetomimid. The preopercular canal has four to five pores and three to four neuromasts in all cetomimids except some species of *Gyrinomimus*; in one undescribed species there are three neuromasts but two or all three of the overlying skin bridges are undeveloped.

The lateral line system on the trunk in all genera except *Procetichthys* and *Rhamphocetichthys* consists of a wide canal sloping gradually from the top of the gill opening to the base of the caudal fin posterior to the hypural bones. This type of main trunk canal is the complete (straight) pattern, considered primitive for teleost fishes (Webb, 1989). The canal is pierced by a series of large pores (that are often smaller on the posterior third of the canal), which differ in number and shape among taxa. The largest pores are as wide as the lateral line canal and can be so extensive that the canal is reduced to a series of small bridges of skin over the lateral line neuromasts and scales; in a few species the posterior pores are less than one quarter the width of the canal. The last pore, however, is usually as wide as the tube itself. Various keels and flaps project from the lateral wall of the canal between pores in some species of the genera *Cetomimus*, *Gyrinomimus* and *Cetostoma*, and can be quite extensive. The pores, flaps and superficial neuromasts are best observed with the specimen submerged in liquid.

A series of small to large, thin scales lies in the floor of the lateral line canal. The number of scales and overlying neuromasts is one less than the number of lateral line pores, as one scale is present in the area between two pores. The pore counts were determined by counting scales and adding one when the lateral wall of the canal was lost. The shape of the scales differs among taxa, with the most elaborate scales in *Cetomimus* and *Gyrinomimus* having dorsal and ventral projections that support the sides of the lateral line canal (Fig. 5c). The entire series of scales were examined in each of the cleared and stained specimens and a section of lateral line canal containing three or four posterior scales was removed from at least one specimen of most genera and cleared and stained. The scales begin just behind the supracleithrum and extend the length of the canal to just anterior to the terminal pore. All of the scales are thin and weakly ossified, although the posterior scales are somewhat more ossified than the anterior scales in some species. None of the cephalic canals have scales (although most of the circumorbital bones underlying the infraorbital canal are similar to the lateral line scales, with a median foramen). Each lateral line scale is pierced by a median foramen, through which runs a branch of the underlying lateral line nerve. The neuromasts sit on top of the scales in

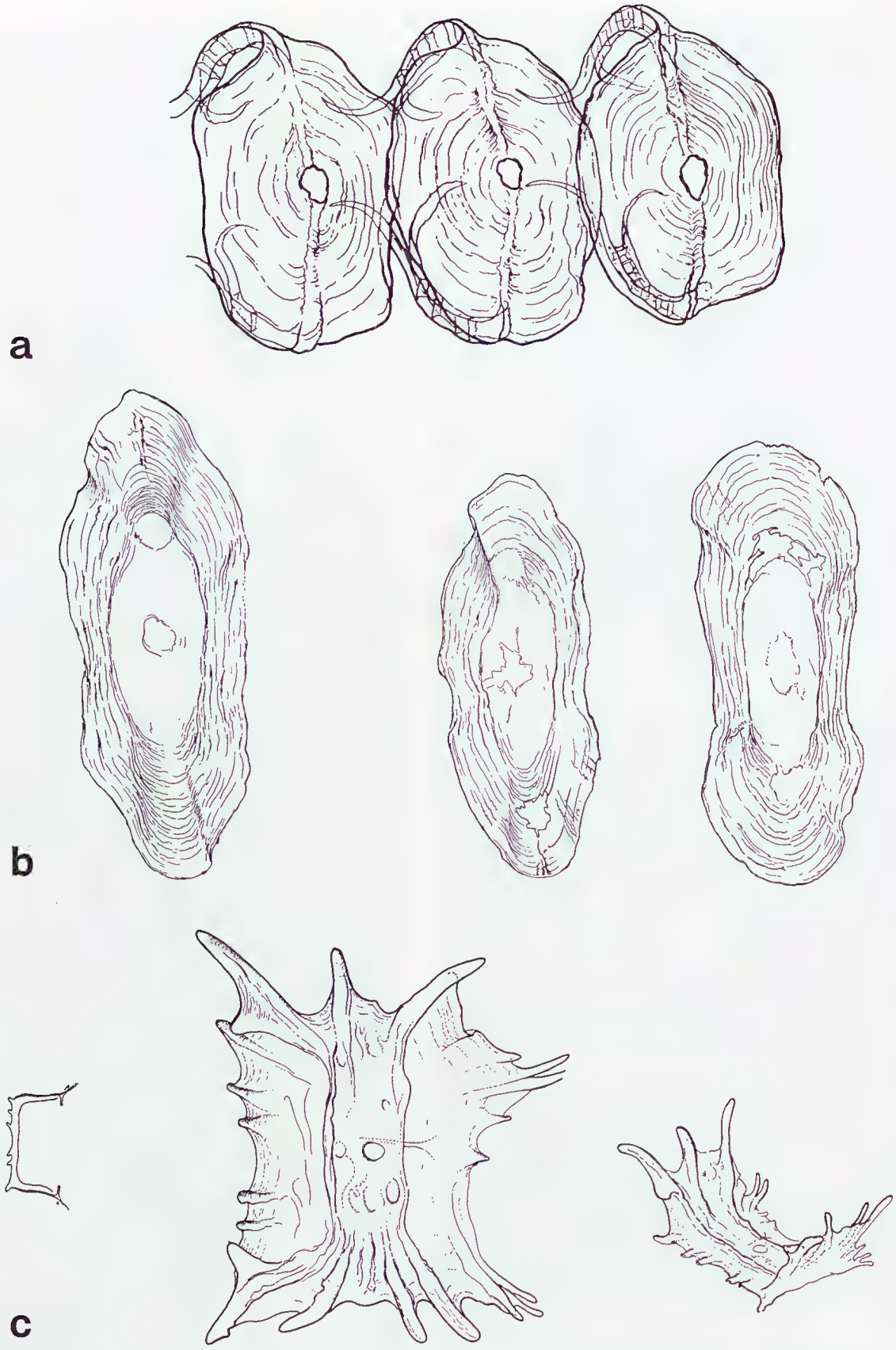

Fig.5. Lateral line scales; a, *Barbourisia rufa*, 133 mm, AMS I.27261-001, medial view of left scales 29-31, anterior to left; b, *Ditropichthys storeri*, 83 mm, AMS I.18821-001, lateral view of left scales 10-12, anterior to left; c, *Gyrinomimus* sp. B, 358 mm, ISH 1115/79, posterior, lateral and three-quarter views of right scale 19.

the floor (median wall) of the lateral line canal. These internal lateral line scales are not similar to the external lateral line scales found in most bony fishes, as the lateral line canal runs over the entire scale, not through a pore in the scale.

In *Procetichthys* and *Rhamphocetichthys* no lateral line canal is present on the body. The lateral line consists of vertical rows of papillate superficial neuromasts, from one to many in the former genus (Fig. 6b) and usually three in the latter. In both genera a series of buried scales underlie the papillae.

Numerous large and small papillae are found in various regions of the head, trunk and caudal fins. These appear to be papillate superficial neuromasts, of which the distribution and nomenclature have been summarised by Coombs *et al.* (1988); their nomenclature is based on innervation and position and is adopted here. It has not been possible to compare the cephalic superficial neuromasts in all cetomimid genera, because of their fragile nature; they seem to be one of the first features lost when whalefishes are abraded in the net. Some generalities are possible, based on those genera with undamaged specimens. One to four rows of papillae cross the snout, representing either or both the supraorbital rostral replacement line and/or the rostral fork replacement of the infraorbital canal line (Coombs *et al.*, 1988: fig. 22.11, tables 22.3-4). A row of papillae from the posterior nostril to above the eye represents the supraorbital accessory line. A vertical row of widely spaced superficial neuromasts anterior to the preopercular canal may represent the dorsal and/or median mandibular lines, while papillae on the posterior lower jaw dorsal to the mandibular canal presumably represent the ventral mandibular line. Opercular papillae appear to represent the dorsal and ventral opercular lines. A small row of papillae anterior to or in the first pore of the mandibular canal is the rostral mandibular replacement line. Scattered groups of superficial neuromasts are typically present medial to the main canal and posterior to the fifth supraorbital canal pore; a study of innervation will be required to establish which of the four possible lines are represented.

The papillate superficial neuromasts on the body are in fewer groups and display less variation than those on the head. A dorsal trunk line appears to be present in all taxa, extending from the back of the head just below the dorsal midline to near the dorsal fin origin. In some species the line of neuromasts is so close to the dorsal midline, with neuromasts from the other side alternating in position, that they appear to form one wavy line posteriorly. The total number of neuromasts ranges from less than ten to more than 30. Papillate superficial neuromasts are also associated with the main trunk canal in all taxa where the latter occurs. Papillae are present on the dorsal and/or ventral margins of the lateral line pores, usually two or less per pore, and on the skin bridges between pores where these are large and well developed. The distribution patterns of superficial neuromasts on the lateral line canal differ among taxa. Finally there is a curved row of papillae on the basal quarter of the caudal fin behind the posterior opening of the lateral line canal. This caudal line of neuromasts, varying from less than one to about one organ per fin ray, usually extends from the top quarter to the bottom quarter of the fin and is present in all taxa.

Cavernous tissue. Harry (1952:57, 58, 70, fig. 2) first described the cavernous tissue in cetomimids. The tissue was considered luminous because of its similar appearance to the luminous caudal organ of *Saccopharynx harrisoni* (Beebe, 1932). Harry (1952) suggested that the cetomimid cavernous tissue secretes a mucous layer which covers most of the head and body with red luminescence. Unfortunately no cetomimid has been captured alive to confirm this hypothesis. Nielsen & Bertelsen (1985) described and figured the caudal organs of all nine species of *Saccopharynx* and figured a microscopic section of the caudal luminous organ of *S. ampullaceus*. Based on the single observation of luminescence in a living specimen of *S. harrisoni* by Beebe (1932), dorsal and ventral photogenic

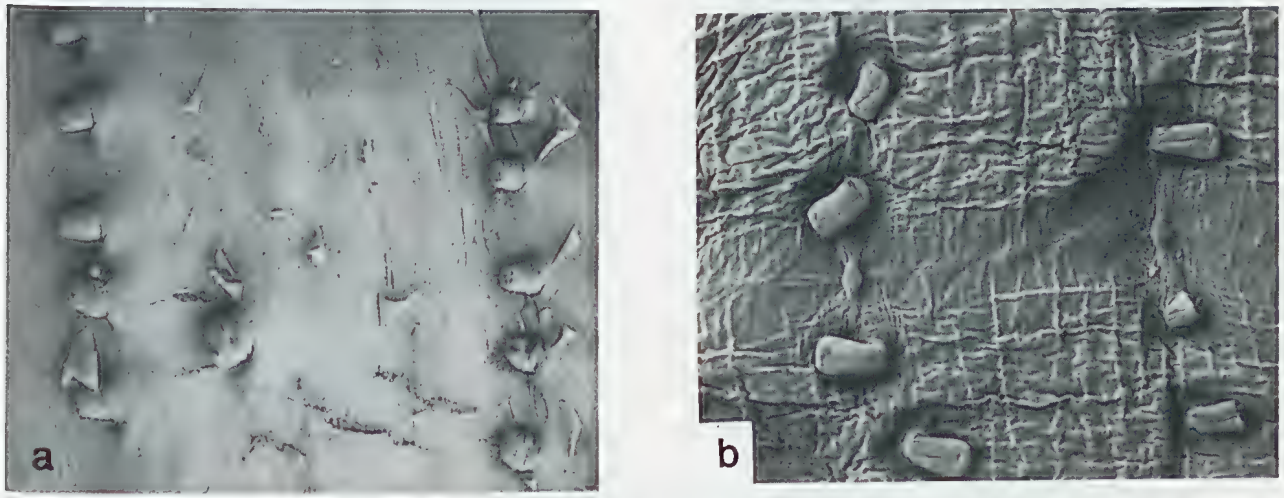

Fig.6. Lateral line neuromasts, right side, anterior to right; a, *Rondeletia loricata*, 83 mm, AMS I.21141-001 (flaps of skin = artefacts of preparation); b, *Procetichthys kreffti*, 236 mm, ISH 1188/71, magnifications approximately 25x; SEM photos D. Hughes, University of Sydney.

tubules with photocytes were identified by Nielsen & Bertelsen (1985), but no reflective tissue nor pigment in the walls of the tubules were found.

Cavernous tissue was dissected from around the anus of *Cetomimus* sp. J and *Gyrinomimus bruuni* and stained and sectioned by Ole Munk of ZMUC; his conclusion was "epidermal tissue of unknown function." The tissue is glandular, with tubules or lobules, but is not microscopically similar to that of *Saccopharynx* (Fig. 7; Nielsen & Bertelsen, 1985: fig. 9). With no evidence that the tissue is luminescent, it is here termed simply cavernous tissue.

Cavernous tissue is developed at least anterolateral to the anus (or the urogenital papilla in *Cetichthys* and *Notocetichthys*) in all cetomimids except *Procetichthys* and *Rhamphocetichthys*. The tissue is most extensive in some species of *Gyrinomimus*, where it may extend over the anal (Fig. 26) and/or under the dorsal fin bases and posteroventral to the pectoral fin base, and *Cetomimus*, where it may occur on the caudal peduncle (Fig. 27), the isthmus, and in one undescribed species as a patch posteriorly on the upper jaw. In *Ditropichthys* an additional small area is present just anterior to the upper portion of the caudal fin.

The cavernous tissue appears more sharply defined and more clearly organised in smaller specimens of all taxa. Within the area around the anus, the cavernous tissue is organised in a series of diagonal rows that are best seen in small specimens of *Danacetichthys*; within each row appear a series of small bundles or tubules (Fig. 20b). In *Gyrinomimus* sp. B, the four known specimens range from 63 to 356 mm SL. While the cavernous tissue covers a larger area in the largest specimen, it is also more superficial and seems to lack the deeply set bundles of white tissue found in the smaller specimens.

Anal lappets, ridges, folds and curtains. A continuous fold of skin hangs over the base of most of the anal fin of *Ditropichthys storeri*. Rofen (1959: 258) mentioned four small lappets over the anterior portion of the anal fin base of *Gyrinomimus bruuni*. These two structures are homologous, being either separate or joined flaps of skin with internal supporting scales originating over the anal fin base, and are here termed the anal lappets. In *Ditropichthys* the anal lappets are continuous, with the outer edge scalloped (Fig. 13). However the internal supporting scales are widely spaced and approximate one per anal ray (Fig. 9). In *Cetostoma* the anal lappets are continuous basally but deeply scalloped distally for about half their width, where they approximate the width of the internal scales (Fig. 21b). In the three other genera where anal lappets occur at least in some species, *Cetichthys*, *Rhamphocetichthys* and *Gyrinomimus*, the lappets are either widely spaced or joined only at the bases (Figs 18b, 26b, 28c). The scales themselves are elongate and very weakly ossified, being thinner and holding less stain than the lateral line scales. In *Cetostoma* the lappets are highly

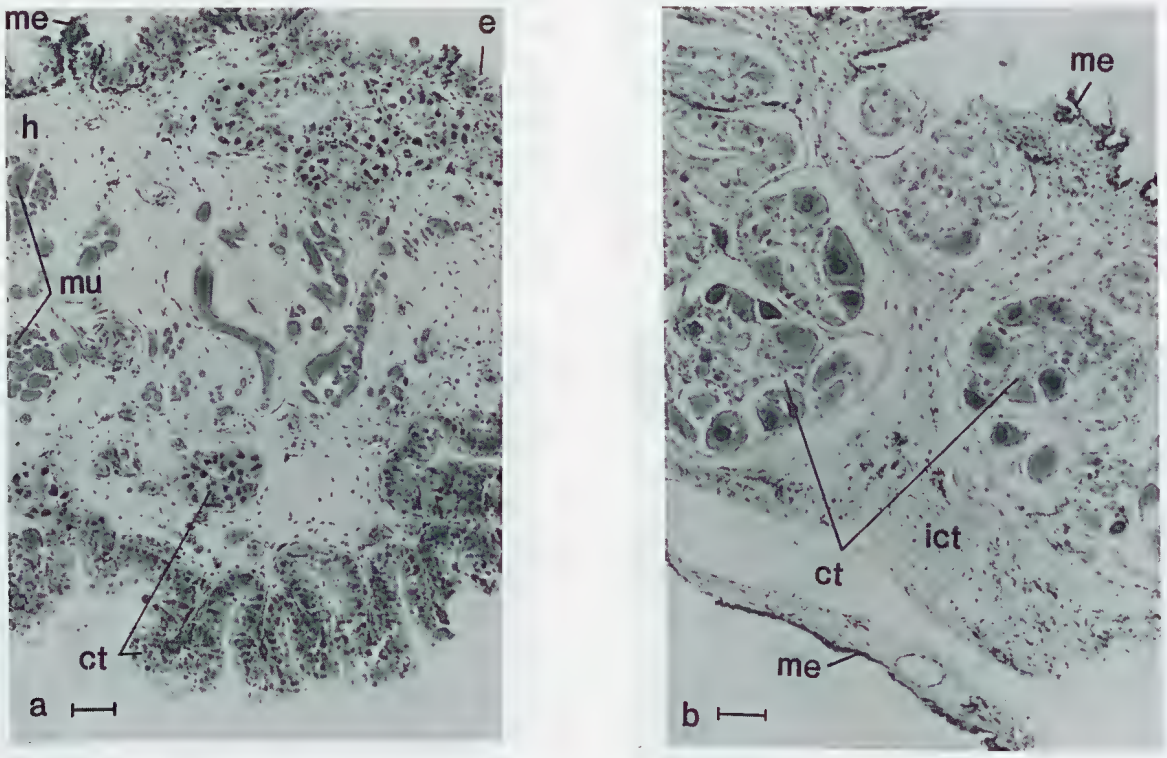

Fig.7. Section of cavernous tissue near anus, stained with haematoxylin and eosin; a, *Cetomimus* sp. J, 90 mm, ZIN 47895; b, *Gyrinomimus bruuni*, 118 mm, AMS I.26870-001; scale bar = 0.1 mm; ct - cavernous tissue, e - epidermis, h - hypodermis or connective tissue, ict - interstitial connective tissue, me - melanophores, mu - muscle; photos R.J. Oldfield, Macquarie University.

vascularised, with numerous presumed blood vessels lateral to the scale (Fig. 21c). In some species of *Gyrinomimus* the cavernous tissue is associated with the anal lappets, extending posteriorly above the anal fin at the base of the anal lappets (Fig. 26b).

The range of number of anal lappets is relatively constant for species, at least in the genus *Gyrinomimus*. In three species the numbers range from ten to 14 (4 specimens), three to six (9 specimens) and four to nine (12 specimens); the number of anal lappets does not increase with size. Unfortunately the lappets are very fragile and easily torn off in capture. None of the 150 specimens of *Cetostoma* had a complete set, and the internal scales of *Ditropichthys* are so thin they can only be counted with assurance if they are cleared and stained with alizarin. In those species with separate anal lappets, small tears in the skin at the anal base are thought to represent the scars of lost lappets. These structures, like the details of the lateral line canal, are best viewed with the specimen submerged in fluid.

In some specimens the anal lappets appear to originate on a low thin ridge of skin. In some instances the ridge may be an artefact of preservation, as the flabby skin is easily moved over the side of the body. In other cases the low ridge is the ventral margin of the cavernous tissue. In a number of specimens of *Cetomimus*, a low, thin skin ridge is present over the anal base, but no anal lappets have been found in any species. In many specimens of this genus tiny ridges run bilaterally down the anterior anal rays. In a few specimens a series of low ridges are present on the membrane between each anterior ray, perpendicular to the rays. These will be described in more detail in the revision of *Cetomimus*.

The skin ridges on the belly of *Cetostoma* do not extend to the anal fin and appear to be associated with the cavernous tissue (Fig. 21c). The diagonal skin ridges of *Notocetichthys* are associated with the middle portion of the lateral line. The two belly keels of *Ditropichthys* are not superficial organs of the skin, but internally based structures.

The posterior portion of the anal fin of *Cetostoma* is voluminous, with extra membrane between the rays creating curtain-like folds. Some vessel-like internal structure within the curtain is apparent.

The function(s) of these unique features remain(s) unknown. The vascularisation of the anal lappets in *Cetostoma* suggests respiration. However vessels are not apparent in other taxa, where in some cases an association with cavernous tissue is indicated. Experimentation with live specimens would help solve the puzzle of these enigmatic structures.

Subpectoral organ. Anteroventral to the pectoral base in *Rhamphocetichthys* is a darkly pigmented structure lying beneath the surface of the skin. In the holotype a pore through the skin appears to be present. This organ is only visible when the overlying skin has faded to a lighter brown, with the organ remaining a darker brown. The subpectoral organ was present in the best preserved

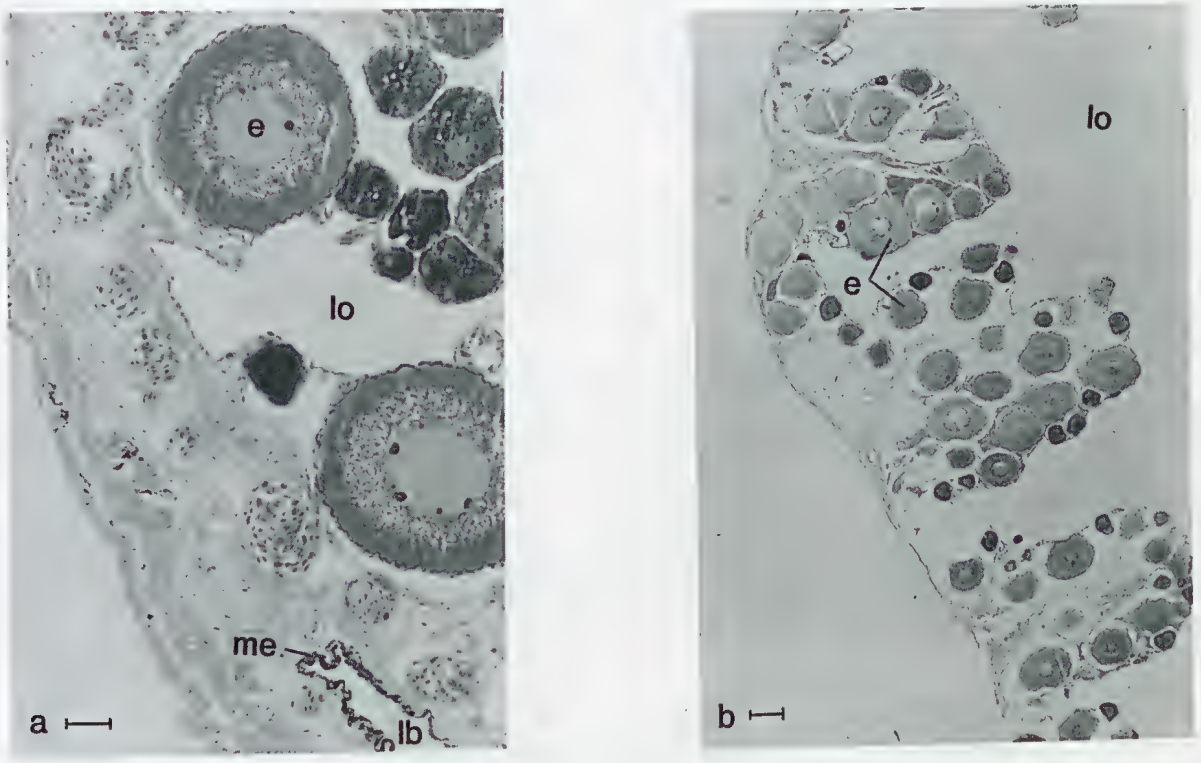

Fig.8. Section of ovary, stained with haematoxylin and eosin; a, Right bladder and ovary, posterior end near junction, *Gyrinomimus grahami*, 310 mm, ISH 398/76(1); b, Posterior ovary, *Ditropichthys storeri*, 112 mm, ISH 607/74; scale bar = 0.1 mm; e - developing eggs, lb - lumen of bladder, lo - lumen of ovary, me - melanophores; photos R.J. Oldfield, Macquarie University.

Fig.9. Anal lappet scales over anal rays 3-6, left side, anterior to left, scale equals 1 mm, *Ditropichthys storeri*, 112 mm, AMS I.27260-001.

specimens of *Danacetichthys* and only in some small specimens of *Cetostoma* and some species of *Gyrinomimus* and *Cetomimus*. It appears best developed in the smaller specimens and does not proportionally increase in size with growth. No indication of an open pore is present in larger specimens. Sectioning of the subpectoral organ from specimens specially fixed upon capture will be required to determine details of its structure and function.

Internal anatomy. Most specimens were dissected to examine gonads. The length of the gonad was measured *in situ* with dial calipers under a dissecting microscope, and the widest point, usually near the anterior end, was occassionally measured; both measurements are accurate only to 0.5 mm. The size of eggs was noted, usually measured with an ocular micrometer, as well as any distinctive features. Routine examination of numerous specimens failed to reveal any obvious males.

Gonads and associated tissues of eight specimens representing four genera and species were embedded, sectioned and stained with haemotoxylin and eosin. All but one of the specimens were at least half of the maximum size recorded for the species, ranging from a 59 mm *Ditropichthys storeri* to a 310 mm *Gyrinomimus grahami*. In every case the gonads were ovaries, with eggs in various stages of development (Fig. 8). Sections were made through all areas of the gonads and no testicular tissue was found. Microscopic examination up to 50 times magnification of numerous dissected specimens, including almost the full size ranges in *Ditropichthys* and *Cetostoma*, failed to reveal any obvious male gonads. Future study will section the gonads of specimens in the smaller half of the size range before hypothesising on where the male cetomimids may be hiding.

One structure that resembled a testis was found to be a thick-walled urinary bladder. In some specimens, ducts (ureters?) appeared to lead to the posterior kidneys. The histology of these organs was that typical of bladders (Fig. 8a). The bladders took a variety of forms in different taxa: usually but not always paired, usually thick walled but occasionally very thin walled, and often coiled and covered with pigment. The bladders, when paired, arise from the lateral surface of the posterior ovary, extend anteriorly into the abdominal cavity and posteriorly exit behind the anus.

Where stomachs were obviously distended, or contents showed up on x-rays, stomach contents were removed for identification. Dissection of all stomachs was not attempted and fewer than 10% of the specimens were analysed in order to determine general feeding preferences for each genus.

No detailed comparative studies of the digestive tracts were attempted. Limited dissection revealed that all members of the family apparently lack pyloric caeca, the intestine arises from the anterior end of the stomach and increases in relative length and number of folds with age. The length of the oesophagus anterior to the stomach appears longer in *Cetostoma* than in other genera. Some comparisons were systematically noted. The amount of melanin pigment covering the stomach and peritoneum varies considerably, from none to complete heavy covering. Also the shape and size of urinary bladder(s) dorsoposterior to the gonads were noted. The position of the anus relative to the anal fin origin varies considerably in different genera, but was measured externally.

Colour. Herring (1975) described the pigmentation of the Cetomimidae, Barbourisiidae and Rondeletiidae. The orange-red pigments found beneath the skin along the myotomes and lateral line in the cetomimid genera *Cetostoma* and *Gyrinomimus* were identified as the carotenoid pigment astaxanthin and its esters. The same pigments were found in all three families. However, in the cetomimids and rondeletiids the skin is also heavily pigmented with melanophores that combine with the underlying carotenoid pigments to give an overall brownish hue, while *Barbourisia* is orange-red in colour because it lacks melanophores. Herring (1975) made his observations on fresh and frozen specimens.

The carotenoid pigments are completely bleached in alcohol and preserved specimens retain no orange colour. The melanin in the epidermis also fades with time; light speeds the fading and weaker rather that stronger concentrations of alcohol also appear to increase fading. While some specimens appear black when freshly caught, all preserved specimens are some shade of brown. Although there appear to be differences in the colour of freshly caught cetomimids, the subjective nature of these observations is compounded by the fullness of the stomach (stretched skin is lighter than loose skin), the often battered condition of the specimens and the time in alcohol. While colour may be of value if quantified for fresh or frozen specimens, only the preserved colour is mentioned in the descriptions and is not considered in the phylogenetic analyses.

Artificial Key to the Genera of Cetomimid Fishes

1. Nasal rosette long, filling both nostrils, with more than 30 large lamellae (Fig. 1e); lateral line without canal and pores, consisting of vertical rows of papillae with at least 8 papillae per row posteriorly; jaw teeth small, widely spaced and sharply pointed in 1-2 uneven rows (Fig. 2a); pseudobranch present; pectoral rays 15; principal caudal rays 19 ..... *Procetichthys*

------ Nasal organ small and short, mostly in anterior nostril, with no or less than 10 small lamellae (Fig. 1f-k); lateral line consisting of a canal with pores or vertical rows of papillae with less than 5 papillae per row; jaw teeth tiny and triangular or elongate, closely spaced in 3-10 rows (Fig. 2b-f); pseudobranch absent; pectoral rays 17-24; principal caudal rays 12-16, rarely 17 2

2. Dorsal rays 29-37; anal rays 26-34; dorsal and to a lesser extent anal fins abruptly elevated on bases higher than body; slit behind angle of fourth gill arch tiny and tubular; 3 separate copular tooth plates; fin membrane between last 10 anal rays voluminous and curtain like; snout-dorsal origin 1.7-2.0 in SL ..... *Cetostoma*

------ Dorsal and anal rays 12-21; dorsal and anal fin bases not abruptly elevated above body; slit behind ventral arm of fourth gill arch either elongate or absent; 1 copular tooth plate; fin membrane between posterior anal rays not voluminous and curtain like; snout-dorsal origin 1.3-1.6 in SL 3

3. Snout elongate and beak-like, 5.1-6.2 in SL; no lateral line canal with pores, but vertical rows of 1-3 papillae; no lateral line system of canals on head, only sensory papillae; no cavernous tissue around anus; gill arches 2 and 3 without tooth knobs or plates; underlying lateral line scales 31-40 ..... *Rhamphocetichthys*

------ Snout not elongate and beak-like, rounded, 6.9-12.7 in SL; lateral line a canal with 9-25 pores, no vertical rows of papillae; lateral line system on head with canals and pores; cavernous tissue anterior to or around anus, often elsewhere; gill arches 2 and 3 with tooth plates or knobs; underlying lateral line scales 8-24 4

4. Free gill arches 4, with gill slit behind ventral arm of fourth gill arch; gill tooth plates separate and raised, club shaped to domed (Fig. 3b-d); lateral line scales round to rectangular and flat, without dorsal and ventral projections; vertebrae 38-46 5

------ Free gill arches 3, with no gill slit behind ventral arm of fourth gill arch; gill tooth plates contiguous, fusing with age, flat (Fig. 3e-h); lateral line scales elongate and curved with dorsal and ventral projections supporting lateral line canal; vertebrae 44-59 8

5. All jaw teeth in distinct longitudinal rows, elongate with length more than 3 times basal width; gill arch tooth plates elliptical and slightly raised; premaxillary length 3.2-3.4 in SL; ventral pharyngeal tooth plates present; lateral line scales (=pores - 1) 17-18; vertebrae 43-46 ..... *Danacetichthys*

------ Jaw teeth in indistinct diagonal or longitudinal rows, with only inner row elongate or all tiny and triangular with length less than 2 times basal width; gill arch tooth plates on club-shaped gill rakers or raised rounded knobs; premaxillary length 3.5-5.2 in SL; no ventral pharyngeal tooth plates; lateral line scales 10-16; vertebrae 38-43 6

6. Dorsal rays 19-23, dorsal base 3.8-4.8 in SL; anal rays 15-18, anal base 5.1-6.6 in SL; lateral line scales rectangular; flap of skin with internal anal lappet scales over base of anal fin; cross section of belly posteriorly truncate with 2 ventral ridges; anus very close to anal fin origin, distance 23-100 in SL; palatine teeth present; ectopterygoid tooth plate long, extending to or slightly before rictus; gill rakers fully developed, club shaped ..... *Ditropichthys*

------ Dorsal rays 13-16, dorsal base 5.8-8.5 in SL; anal rays 11-14, anal base 7.0-14.1 in SL; lateral line scales round; no flaps of skin with internal anal lappet scales over anal fin; cross section of belly posteriorly rounded with no ventral ridges; anus far anterior to anal fin origin, distance 10-20 in SL; palatine teeth absent; ectopterygoid teeth absent or patch very short, ending far before rictus; gill rakers as very short knobs 7

7. Lateral line scales 15-16; cavernous tissue between anus and anal fin with free posterior margin and long, free posterior extension; 5-7 diagonal skin ridges on midbody, each ridge passing over lateral line scale; vomerine and ectopterygoid teeth absent; copular tooth patch very short, 90-110 in SL, beginning behind level of eye; gill rakers on first arch 2+8; holobranchs on gill arches 1-4 long and closely spaced ..... *Notocetichthys*

------ Lateral line scales 8-14; cavernous tissue anterior to anal fin origin, without free posterior margin or extension; no diagonal ridges of skin on midbody; vomerine and ectopterygoid teeth present; copular tooth patch long, 8.5-25 in SL and beginning before level of eye; gill rakers on first arch 3+7-10; holobranchs on gill arches 1-4 very short and widely spaced ..... *Cetichthys*

8. Jaw teeth in distinct longitudinal rows (indistinct diagonal rows in smallest specimens of 2 species), all but newest teeth elongate with length more than 3 times basal width; vomerine tooth plate flat and rectangular or oval ..... *Gyrinomimus*

------ Jaw teeth in indistinct diagonal rows, all teeth short with length less than 2 times basal width; vomerine tooth plate domed and round or rarely oval ..... *Cetomimus*

Diagnoses and Descriptions

Family Cetomimidae Goode & Bean, 1895

Diagnosis. Body soft and flabby, whale shaped with dorsal and anal fins far posterior and opposite; no body scales; head large to very large, less than 5, usually less than 4 or 3, in SL; mouth enormous, extending far behind eye, less than 2 in head length, end of premaxilla usually closer to posterior margin of operculum than eye; eye tiny, usually degenerate without lens in specimens over 100 mm SL, less than 10 in HL in small specimens, less than 20 in HL in larger specimens. No supramaxillae, orbitosphenoid or subocular shelf; palate usually toothed; 3 or 4 free gill arches; ventral pharyngeal tooth plates of fifth ceratobranchial present or absent; copular tooth plate present, very short, or broad and shield shaped or very long and narrow, single or as three separate plates; pseudobranchiae usually absent; gill rakers club shaped, or as toothed knobs, tooth plates or individual teeth. No pelvic girdle or fins. No fin spines; almost all rays segmented, most dorsal, anal and caudal rays usually branched; dorsal and anal fins with 11-37 rays; caudal fin with 10-19 principal rays; pectoral fin with 15-24 rays; pectoral girdle reduced, with unforked post-temporal (not confirmed in all taxa). Vertebrae 38-59; second preural centrum usually with double neural and haemal spines. Lateral line a broad tube pierced by large pores, or series of vertical rows of papillate superficial neuromasts; 2 parallel rows of superficial neuromasts anterior to dorsal fin; scales present beneath lateral line organs; lateral line system of head a series of cavernous canals with moderate to large pores in all taxa except one. Stomach highly distensible; no pyloric caeca; no pleural ribs; no predorsal bones. Colour brownish-black mixed with reddish orange, resulting from carotenoid pigment astaxanthin and its esthers and melanin; cavernous tissue usually present around anus, sometimes at fin bases and other areas.

Subfamily Procetichthyinae n.subfam.

Diagnosis. This monotypic subfamily differs from all other known cetomimids in having large nasal organ with

well-developed olfactory lamellae; connection between infraorbital canal of lateral line system and posterior nostril; eye with well-developed lens in specimens over 100 mm; 1-2 uneven rows of small, widely-spaced jaw teeth; small pseudobranch; only 15 pectoral rays; lateral line system on body incorporating vertical rows of papillate superficial neuromasts with at least 8 papillae in each row posteriorly without overlying tube or pores; caudal fin with 19 principal rays; peritoneum unpigmented.

Content. A single genus and species.

Procetichthys n.gen.

Type species. *Procetichthys kreffti* n.sp.

Diagnosis. As for the subfamily.

Description. D. 14; A. 13; P. 15; principal C. 19; vertebrae 48; trunk canal lateral line organs 86. Size large, attaining at least 236 mm; head large, 3.3 in SL, and wide, width at eye 2.5 in HL; mouth very large, jaws ending much closer to opercular margin then level of eye; snout rounded and moderate, 2.7 in HL; dorsal and anal bases short, 1.9-2.4 in HL; caudal peduncle long, 1.5 in HL and moderately deep, 2.7 in CPL; anus moderately anterior to anal fin origin, distance 1.1 in CPD.

Nasal organ large with well-developed olfactory lamellae. Eye small, 29 in HL, but with well-developed lens. Lateral line system of head a series of large canals with wide pores; supraorbital canal with 7 pores joined to main canal with 3 pores; infraorbital canal with 8 pores, not joined to main canal, last neuromast not displaced; mandibular canal with 7-8 pores, not joined to preopercular canal; preopercular canal with 4-5 pores and 3 neuromasts; neuromasts of head large, flat, diamond shaped. Lower jaw without lateral or ventral spines posteriorly. Jaw teeth small, widely spaced and sharply pointed in 1-2 uneven rows; 2 vomerine teeth; palatine and ectopterygoid teeth confluent, extending almost to rictus; copular tooth patch on 1 plate, moderately long, length 3.2 in HL, and narrow width, 13.9 in length.

Free gill arches 4, with small slit behind ventral arm of fourth arch; holobranchs well developed on all 4 arches, present on all of dorsal arm of first arch; small pseudobranch present. Gill rakers as small canine teeth on first 3 arches, none on medial face of gill arches; ventral pharyngeal tooth plates present.

Lateral line a series of vertical rows of papillae, 1-3 per row anteriorly and 8-18 per row posteriorly; no lateral line tube with pores; lateral line scales flat and narrow. No cavernous tissue. No subpectoral organ. No abdominal ridges or diagonal midbody ridges. No lappets, ridges, folds or membranous curtain associated with anal fin. Stomach unpigmented.

Etymology. From the Greek *pro* - first, *cetus* (*ketos*) - whale, *ichthys* - fish, in reference to its primitive sister group relation to other whalefishes. The gender is masculine.

Remarks. Only one specimen of the genus has been collected, in bathypelagic waters of the south-eastern Atlantic.

Procetichthys kreffti n.sp.

Figs 1e, 2a, 3a, 4a, 6b, 10-12

Type material. HOLOTYPE: ISH 1188/71, 236.5 mm female, *Walther Herwig* 412-II/71, south-east Atlantic, 37°08'S, 5°23'E, 0-2200 m, 192-2400 hrs, 21 Mar. 1971.

Diagnosis. As for the subfamily.

Description. The only known specimen is in moderate condition with the body wall torn open anterior to the anal fin and behind the pectoral girdle on one side. Most of the skin and fin ray tips are present. The anterior third of the left premaxilla is lost and the head is distorted.

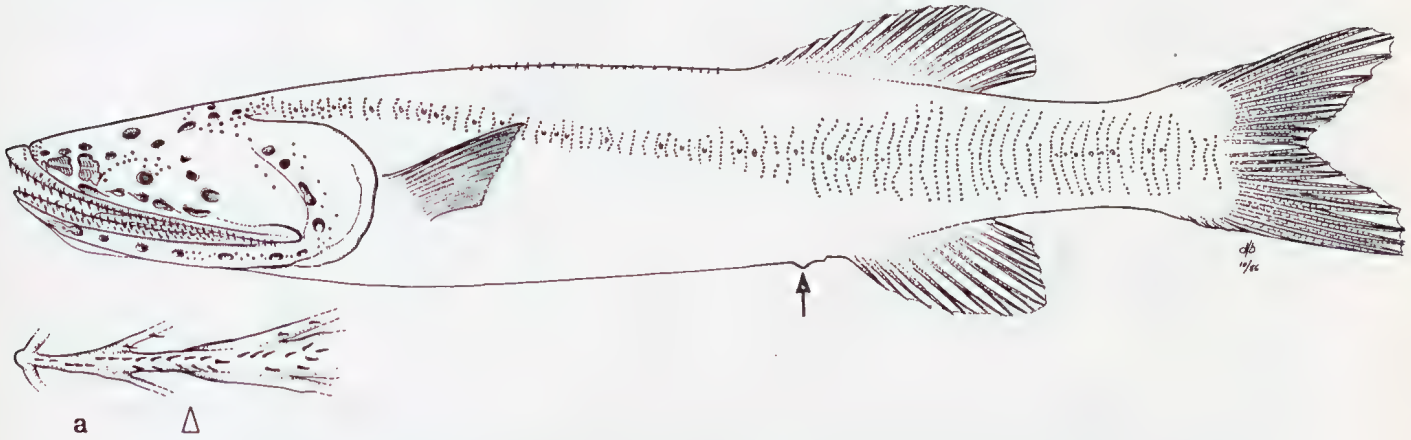

Fig.10. *Procetichthys kreffti* holotype, 236.5 mm, ISH 1188/71, arrow indicates level of anus; a, teeth on copula (not to scale), triangle indicates level of eye.

D. 14; A. 13; P. 15; principal C. 10+9; procurrent C. 8+7; vertebrae 28+20=48; vertical rows of lateral line neuromasts 39 from under dorsal origin to caudal; trunk canal lateral line organs 86. Measurements in Appendix Table 9.

Body oval in cross section behind head; greatest depth midabdominal. Caudal peduncle much longer than deep. Anus anterior to anal fin origin by distance approximately equal to caudal peduncle depth. Skin around anus damaged, no apparent cavernous tissue. Very slight mid-dorsal ridge from dorsal origin halfway to head; no apparent midventral ridge. No anal lappet flaps, scales or ridges at anal fin base. No pore or pigment patch of subpectoral organ visible.

Head large, depressed anteriorly and compressed posteriorly, wider than deep at level of eyes, deeper than wide at rictus. Head and body profile very slightly rounded from snout to dorsal origin. Nostrils very large, much larger than lateral line pores or eye, with raised anterior rim; nasal organ large, elongate with about 35 fully developed olfactory lamellae on each side of central raphe (Fig. 1e); internasal bridge of skin equal to horizontal diameter of posterior nostril; line between tip of snout and eye passes midway through each nostril; small canal connecting posterior nostril with infraorbital canal of lateral line system. Eye small, with well-developed lens, midway between upper jaw and snout profile; interorbital broad, smooth, convex. Mouth enormous, moderately oblique; dentigerous margin of upper jaw straight posteriorly, convex anteriorly, that of lower jaw concave; rictus approximately 2 eye diameters before posterior tip of premaxilla; posterior end of jaws well before end of gillcover, without spines or processes. Jaw teeth well spaced in 1 or 2 rows; individual teeth relatively long, recurved, non-depressible cones with sharply pointed tips (Fig. 2a); upper jaw teeth 40, in single row beginning about 1 eye diameter behind symphysis and extending along entire length of premaxilla, behind rictus, plus 2 larger canines on either side of symphysis; lower jaw teeth in 2 rows commencing just behind symphysis; outer row of 31-33 smaller canines decreasing in size posteriorly and extending to 1 eye diameter before rictus; inner row of 35-37 canines extending to rictus. Palatal teeth similar to jaw teeth; 2 canines on vomer; palatine-ectotperygoid teeth in 1 row commencing 2 eye diameters behind vomer and extending almost to level of rictus, 28 teeth on one side (broken on other), slightly decreasing in size posteriorly; division between palatine and ectopterygoid indistinguishable. Teeth on copula, pharyngeals and gill arches all similar to jaw teeth except smaller and depressible; copular tooth patch long and slender, with 1 row of teeth anteriorly and 2 rows posteriorly, 18-19 teeth longitudinally; length of copular patch about 1.2 in snout.

Free gill arches 4, small slit about length of eye diameter behind ventral arm of fourth arch; dorsal arm of first arch free, half of dorsal arm of second and all of dorsal arms of third and fourth arches bound in skin of gill chamber. Holobranchs well developed, closely spaced, those on ventral edge of first gill arch about 3 times width of arch (Fig. 3a); holobranchs of fourth arch about four fifths as long as those of first arch; holobranchs present on dorsal arm of all 4 arches; small pseudobranch present, of 3-4 filaments, the second largest and slightly longer than width of first gill arch. Normal gill rakers absent; first arch with 5-6 hypobranchial, 5 ceratobranchial and 4 epibranchial tooth patches evenly spaced plus 1 tooth in angle of arch;

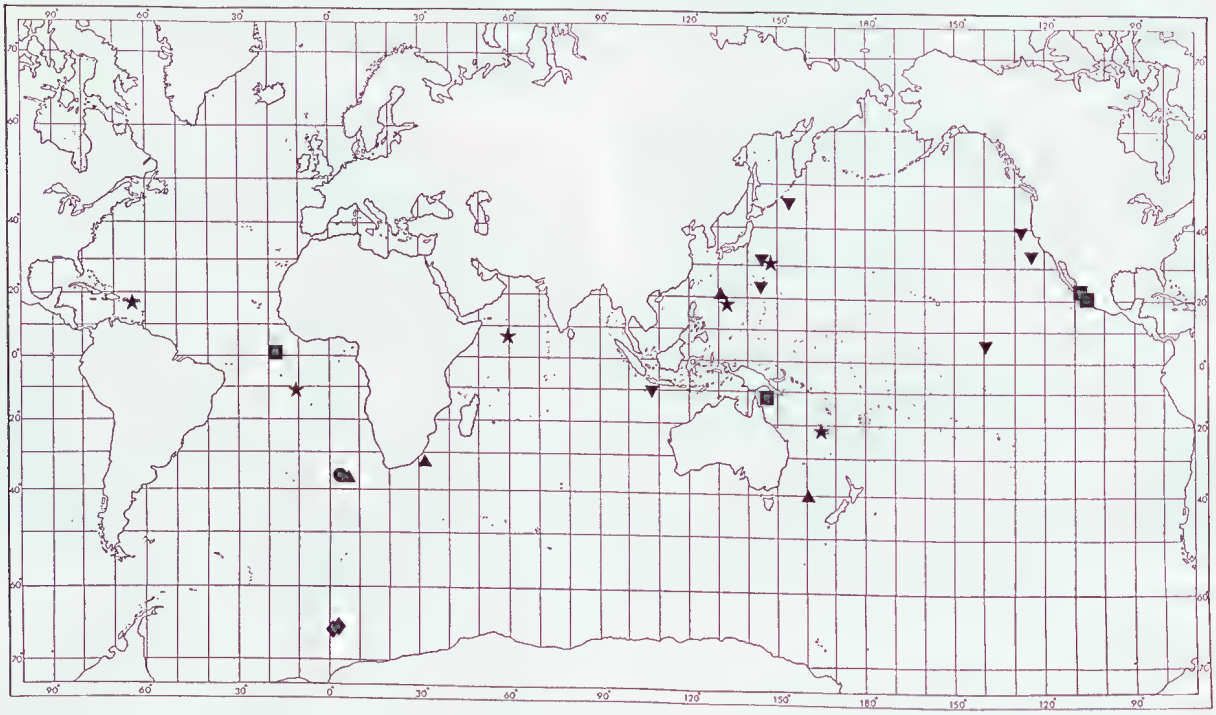

Fig.11. Horizontal distribution of *Procetichthys kreffti* (closed circle), *Cetichthys indagator* (triangle), *C. parini* (inverted triangle), *Notocetichthys trunovi* (diamond), *Danacetichthys galathenus* (star) and *Rhamphocetichthys savagei* (closed square).

hypobranchial patches of 1-2 teeth, ceratobranchial teeth all single and epibranchial patches of 1-3 teeth (Fig. 3a); second arch with 8 small canines on ventral arm, third arch with 3 teeth ventrally, fourth arch edentate; no teeth on medial faces of arches. Dorsal pharyngeals as 2 pharyngobranchial tooth plates on each side of roof of mouth, anterior (third pharyngobranchial) plate with 7-8 teeth arranged in triangular patch, posterior (fourth pharyngobranchial) plate with 15-17 teeth in oval-shaped patch; paired ventral pharyngeals (fifth ceratobranchials) as elongate triangular tooth plates with 19-20 teeth.

No indication of tube pierced by pores in lateral line. Lateral line system complex (Figs 6b, 10), consisting of 86 lateral line organs in longitudinal row from top of gill opening to base of caudal rays; these organs in very shallow groove approximately half an eye diameter wide, with bottom of groove smoother than skin of either side; each lateral line neuromast associated with vertical row of papillate superficial neuromasts; posterior rows longer with more papillae; from row 51 just posterior to anal origin to row 82 just before caudal base, number of papillae range from 13-18 per row with 6-10 papillae dorsal and ventral to main neuromast, except for 3 shorter rows with 8-12 total papillae; rows 83-85 on caudal base with 8-10 papillae each, while last uneven row on caudal rays with 17; rows 40-50 with 4-11 papillae, rows 1-39 with 1-6 total papillae per row; each papilla in a shallow pit of smoother skin; larger papillae, 2-3 times the size of those in vertical rows, in main depression of lateral line, organised approximately every 2 rows in space between rows; 31 larger papillae from opercular opening to row 50, none behind; both larger and smaller papillae with nerve running to opening at tip of papillae and joining lateral line nerve overlying muscle mass under skin; branches of nerve also entering each main lateral line neuromast; although solidified mucous in center of most main neuromasts and some larger papillae, no microstructure evident at 50 times magnification. Lateral line scales narrow and flat in underlying connective tissue. Two parallel rows of superficial neuromasts, similar in size and shape to those of vertical rows of lateral line, the dorsal trunk line, in dorsal midline from level of gill openings to just before dorsal origin, 32/40 papillae per row.

Lateral line system on head of deep cavernous tubes

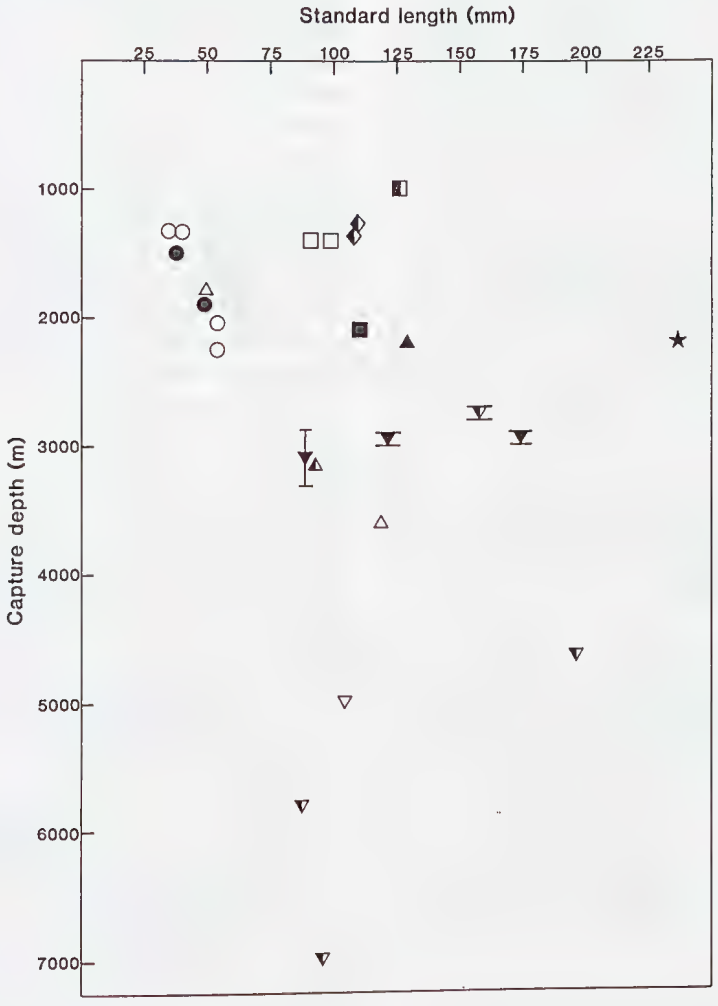

Fig.12. Vertical distributions of *Procetichthys kreffti* (star), *Cetichthys indagator* (triangle), *C. parini* (inverted triangle), *Notocetichthys trunovi* (diamond), *Danacetichthys galathenus* (circle) and *Rhamphocetichthys savagei* (square); open symbols indicate day captures, solid symbols night captures, half solid symbols day/night or unknown time, depths are maximum fishing depths of open nets; closing net captures indicated by vertical bars giving fishing depth limits.

with moderate-sized pores (Fig. 4a); neuromasts large, flat, diamond shaped on floor of canals. Supraorbital canal from snout to behind eye, with 7 pores and 6 neuromasts, 5th pore largest but far from dorsal midline, anterolateral bend after 5th pore joined to main canal with 3 pores and organs, supratemporal pore medially joined to 2nd pore. Infraorbital canal not joined to main canal, with 8 pores and 8 neuromasts, 7th organ not displaced anteriorly, 8th pore behind eye; connection between 1st infraorbital pore and posterior nostril, with neuromast in floor of small joining canal. Mandibular canal with 7-8 pores (skin bridge between anterior 2 pores only partially formed on one side) and 7 neuromasts plus 3 large papillae in floor of elongate 1st pore; preopercular canal not joined to lower jaw canal, with 4-5 pores and 3 neuromasts. Three or 4 irregular rows of superficial neuromasts across front of snout, with 15-20 papillae per row; 15-16 papillate neuromasts from behind posterior nostril to over and behind eye, as superficial accessory line; about 15 papillae around last 3 dorsal canal pores; 3 papillae before upper preopercular pores and about 15 papillae on operculum behind pores; about 15 papillae on posterior lower jaw.

Dorsal and anal fins far posterior; dorsal origin slightly before anal origin. Dorsal with 14 rays, 2 simple rays followed by 11 branched rays and 1 simple ray; anal with 13 rays, 2 simple, 10 branched and 1 simple. Pectoral fin moderate in size, directed obliquely upwards, upper rays longest, all rays branched for about distal third of their length. Caudal fin moderately long, strongly forked with 19 principal rays.

The specimen is a mature female with 2 distinct egg sizes; the larger eggs are 1.9-2.0 mm in diameter, the smaller 0.3-0.5 mm in diameter. The overies are ruptured, protruding through the body wall and the details of ovarian structure and urogenital openings could not be ascertained. No testes or bladder are apparent.

Colour in alcohol dark brown, fin tips light brown; mouth, gill cavities, stomach, intestine and peritoneal lining unpigmented.

Distribution. The only known specimen was captured with an open net fishing to 2200 m in the south Atlantic (Figs 11,12).

Etymology. After Gerhard Krefft of ISH, who has organised the world's largest collection of whalefishes and provided hospitality and encouragment for their study, in recognition of his contributions to the knowledge of deep sea fishes.

Remarks. Other specimens of cetomimids taken in the same haul include *Cetichthys indagator*, *Cetomimus* sp., *Cetostoma regani*, *Gyrinomimus* sp. and *G. grahami*.

Subfamily Cetomiminae Goode & Bean, 1895

Diagnosis. Nasal organ small, olfactory lamellae greatly reduced or absent; no connection between infraorbital canal of lateral line system and posterior nostril; eye degenerate, without lens in specimens over 100 mm; 3-10 rows of jaw teeth, either granular, triangular or elongate, never widely spaced; pseudobranch absent; pectoral rays 17-24; lateral line system on body usually with overlying tube pierced by pores; caudal fin with 12-17 principal caudal rays; peritoneum dark brown.

Ditropichthys Parr, 1934

Ditropichthys Parr, 1934: 21. Type species *Cetomimus storeri* Goode & Bean, 1895 by original designation.

Diagnosis. *Ditropichthys* differs from all other cetomimid genera in having fully developed, club-shaped gill rakers, a pair of thin dermal folds along abdomen and anal lappets connected as an unbroken fold of skin containing lappet scales over base of anal fin.

Description. D. 19-22; A. 15-18; P. 17-21; principal C. 6-8+7-8=13-16, counts approximate as all fins damaged; vertebrae 20-24+16-19=38-42 (n=39); trunk canal lateral line scales and organs 10-13. Size moderate, maximum 131 mm; head moderate to large, 2.9-3.4 in SL, and moderate to wide, width at eye 2.3-3.7 in HL; mouth large, jaws ending about midway between eye and opercular margin; snout rounded and moderate, 2.1-3.1 in HL; dorsal and anal bases moderate, 1.2-2.2 in HL; caudal peduncle short to moderate, 1.8-2.4 in HL and slender to moderate, depth 2.0-3.1 in CPL; anus slightly anterior to close to anal fin origin, distance 1.6-6.0 in CPD.

Nasal organ short and high without lamellae. Eye tiny, 14-31 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores, supraorbital canal with 6 pores joined to main canal with 3 pores; infraorbital canal with 8 pores, last neuromast not displaced out of series, contiguous with main canal, but no connecting skinbridge; mandibular canal with 5-6 pores, not joined to preopercular canal with 5 pores; neuromasts of head large, round, firm. Lower jaw with weakly-developed lateral and ventral spines posteriorly. Jaw teeth tiny, closely set in irregular diagonal rows; vomerine tooth patch elongate to oval; palatine teeth present; ectopterygoid tooth plate elongate, extending about to rictus; copular tooth patch on 1 plate, short to moderate with length 4.6-8.6 in HL, and very broad to moderate, width 2.2-6.2 in length.

Free gill arches 4, with slit behind ventral arm of fourth arch; holobranchs well developed on all 4 arches, present on dorsal arm of first arch. Gill rakers fully developed, club shaped, denticulate, on all 4 arches; similar smaller rakers on medial faces of all 4 arches; no ventral pharyngeal tooth plates.

Lateral line a broad tube pierced by wide pores, without flaps or keels; lateral line scales flat and rectangular to oval. Cavernous tissue extensive around anus only. No subpectoral organ visible. Paired fleshy ridges on abdomen. No diagonal midbody ridges present. Anal lappets long and broad, joined together in solid skin fold extending over anal fin base to about anal ray 13-14; no

membranous curtain connecting posterior anal rays. Stomach darkly pigmented.

Etymology. From the Greek *di* - two, *tropis* - keel and *ichthys* - fish, presumably in reference to the folds over the anal fin or the paired abdominal ridges. The gender is masculine.

Remarks. Specimens have been collected in meso- and bathypelagic waters of all three oceans. The genus is monotypic.

Ditropichthys storeri (Goode & Bean, 1895)

Figs 1f, 3c, 4d, 5b, 8b, 9, 13-16

Cetomimus storeri Goode & Bean, 1895: 453, pl. 17(3). Holotype USNM 35634, lost, from the north-western Atlantic, 39°03'N, 70°51'W.

Cetomimus storeri.-Goode & Bean, 1896: 69-70, pl. 21(79) (redescription).-Jordan & Evermann, 1896:550 (redescription).-Brauer, 1906: 252-253, pl. 10(5) (Indian Ocean specimen).-Murray & Hjort, 1912: 613, 681-682, fig. 497 (north-eastern Atlantic specimen).-Parr, 1928: 177, fig. 43 (north-western Atlantic specimen).

Ditropichthys storeri.-Parr, 1934: 21-24, fig. 5 (redescription).-Norman, 1939: 32 (Indian Ocean specimen).-Harry, 1952: 58-59 (2 Bermuda specimens).-Marshall, 1954: 225, 241 (redescription) .-Koefoed, 1955: 3 (north Atlantic specimen).-Rass, 1955: 334-337 (north-western Pacific specimen listed) .-Marshall, 1960: 43, 112 (swim bladder).-Munk, 1965: 22, 26-28, pl. 10(1) (ocular anatomy).-Munk, 1966: 38, 55-56, pl. 15(1) (ocular anatomy).-McAllister, 1968: 98 (hyoid arch).-Craddock & Mead, 1970: 31 (south-eastern Pacific specimen listed).-Marshall, 1971: 144, fig. 50 (lateral line organs).-Kotthaus, 1972: 17 (Indian Ocean specimen); Fitch, 1979: 63-65, fig. 1f (otolith).-Stein, 1985: 190 (north-eastern Pacific specimen listed).

Gyrinomimus bruuni?.-Parin *et al.*, 1974: 114 (Atlantic specimen briefly described).

Material examined. See Appendix Table 3. The following description is based on 26 specimens (26.8-128.5 mm, with an * in Table 3) chosen on the basis of their good condition. The descriptions of such features as fin shape, lateral line pore shape and number of superficial neuromasts is a composite based on different parts of the best specimens. Meristic counts include the range of all specimens examined for which counts were made.

Diagnosis. As for genus.

Description. D. 19-22; A. 15-18; P. 17-21; principal C. approximately 6-8+7-8=13-16, no fins complete enough for exact count; procurrent C. ca. 3-5+3-4; vertebrae 38-42; lateral line scales/organs 10-13. Measurements in Appendix Table 4.

Body oval in cross section, greatest depth at level of pectoral base, becoming compressed posteriorly. Caudal peduncle 2.0-3.1 times longer than deep. Anus usually within 2 mm of anal fin origin. Cavernous tissue strongly developed immediately before anus in roughly triangular-shaped patch joining its fellow from other side in ventral midline, not extending under anal fin. High, thin mid-dorsal keel or ridge from posterior end of head to dorsal origin. Belly with pair of skin ridges/flaps from level of pectoral fin to beginning of cavernous tissue, slightly diverging anteriorly. Body wall below abdominal cavity like

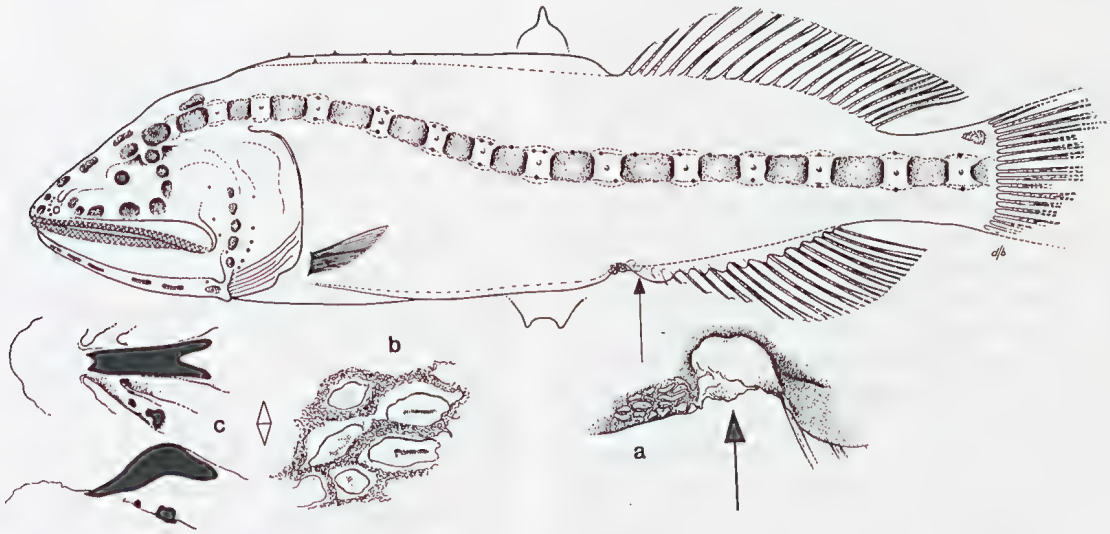

Fig.13. *Ditropichthys storeri*, 131 mm, ISH 1083/71, arrow indicates level of anus; a, b, enlargement of cavernous tissue; c, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye.

truncated triangle in cross section, with apex ventral; thin, solid sheets of muscle laterally between skin and abdominal cavity, ventrally belly keel with 4 separate bundles of muscle running longitudinally and surrounded by white translucent tissue somewhat similar to that found in fishes with indirect luminescent systems (Haneda, 1950); translucent keel extends from cavernous tissue anteriorly to just behind level of pectoral fin base. Very well-developed anal lappet flaps joined together as 1 scalloped flap from anus to base of last 1-5 anal rays, shorter anteriorly and posteriorly; flap supported by weakly ossified scales, flat and elongate, with distal edges making up scalloped edge of flap (Fig. 9); individual scales difficult to count in unstained specimens, numbering approximately 12-17; no indication of scales in belly flaps, which are almost continuous with anal flaps except for interruption of cavernous tissue.

Head very large, deeper than wide, slightly depressed anterior to eye in smaller specimens; head and anterior body profile weakly rounded, outline uneven with bones and pores creating bumps and pits. Nostrils similar to head lateral line pores, midway between tip of snout and eye; anterior nostril round, probably with raised anterior rim in undamaged specimens, half to one third diameter of posterior nostril; internasal skin bridge about as wide as anterior nostril diameter; posterior nostril oval; raphe located entirely in anterior nostril, very short, high, narrow to moderately rounded, lightly pigmented, without lamellae, some specimens with single basal ridge posteriorly (Fig. 1f). Eye small, without lens even in smallest specimens, slightly closer to top of head than upper jaw; interorbital broad, convex and bumpy, narrower in smaller specimens.

Mouth very large, slightly oblique; jaws very slightly concave in undamaged specimens; rictus 2-3 eye diameters before end of premaxilla; posterior end of jaws far before margin of gill cover, closer to level of eye than operculum; lower jaw with weakly-developed lateral and ventral spines posteriorly. Jaw teeth tiny, in a broad band in each jaw, wider anteriorly than posteriorly in irregular diagonal rows, no posterior clumping, extending more than one eye diameter behind rictus in both jaws. Membrane of both jaws very wide and thick, covering most palatal teeth. Vomerine teeth tiny, apparently decreasing in number with increasing specimen size; largest specimens with 5 or fewer teeth, smallest usually with 5-13 teeth, one 32 mm fish with 21 vomerine teeth; patch elongate to oval shaped; in contrast palatine and ectopterygoid teeth increase in number with increasing specimen size; palatine patch elongate, from slightly behind level of vomer to before eye, 1-2 teeth wide in smallest specimens to 5-6 teeth wide in largest; ectopterygoid patch elongate from about level of eye to or slightly before rictus, increasing in breadth (numbers of teeth across) with increasing size; edentate space between palatine and ectopterygoid decreasing with increasing size from half to less than one tenth length of palatine patch as palatine patch increases. Roof of mouth with numerous far-spaced papillae. Copular tooth plate very short and broad, rounded anteriorly and emarginate to lunate posteriorly (Fig. 13c), more elongate and slightly pointed anteriorly in 1 specimen only, domed medially as basibranchials very narrow; teeth tiny, increasing in numbers with increasing size.

Free gill arches 4, with moderate slit behind ventral arm of fourth arch; dorsal arms of first 3 arches free, fourth bound in skin of gill chamber. Holobranchs of all 4 arches well developed, closely spaced, those on ventral arm of first arch about equal to bony width of arch; holobranchs of fourth arch as long as or slightly longer than those of first arch; holobranchs present on dorsal arm of all 4 arches. Club-shaped gill rakers covered with tiny teeth present on all 4 arches (Fig. 3c), numbering 3-4+9-11 on first, 3+8-11 on second, 2-3+6-9 on third and 1-3+5-7 on fourth; 1 specimen with single small tooth patch on fifth arch; similar, smaller toothed knobs project medially from all 4 arches, numbering respectively 10-14, 8-12, 7-10 and 4-7; the numbers do not increase with size and as the size of teeth do not increase with increasing size either, smallest specimens with mouths and gill cavities filled with relatively much larger teeth. Dorsal pharyngeals as pair of large, slightly domed tooth plates covered with tiny teeth; anterior plate elongate, about 2 times longer than wide, rounded anteriorly and truncate posteriorly; posterior plate shorter, half to one third length of anterior, truncate to slightly emarginate anteriorly where it meets anterior plate and rounded posteriorly; plates very closely spaced in comparison to other cetomimids. No ventral pharyngeal plates, except for 1 small tooth patch on fifth ceratobranchial of one side in only 1 specimen.

Lateral line a broad tube with 11-14 pores, without flaps or keels; anteriorly pores almost rectangular, 2-3 times longer than wide with skin bridges over lateral line organs and scales narrow; posteriorly pores more oval with skin bridges wider; 10-13 underlying scales rectangular, oval or diamond shaped, flat or slightly concave, without dorsal or ventral projections, first and last scales usually larger (Fig. 5b); lateral line neuromasts large, round, firm. Skin bridges between pores with 1-3 dorsal and 1 ventral papillate neuromasts and usually 1-2 papillae on dorsal margin of some pores; 2-4 papillae at bases of middle caudal rays behind last lateral line pore; 2 mid-dorsal rows, the dorsal accessory lines, of 8-11 superficial neuromasts from level of upper opercular opening halfway to dorsal origin, rows divergent anteriorly becoming one row posteriorly.

Lateral line system of head with shallow canals, large pores and very large neuromasts under skin bridges between pores (Fig. 4b). Supraorbital canal with 6 pores and 5 neuromasts, with lateral bend at pore 5 joined to main canal with 3 pores and organs plus supratemporal pore and neuromast medial to pore 2. Infraorbital canal with 8 pores and 8 neuromasts, joined to main canal at first pore, skinbridge over neuromast 8 damaged in most specimens, apparently incomplete or absent; neuromast 8 not displaced anteriorly or dorsally out of series. Mandibular canal with 5-6 pores and 4-5 neuromasts, pores much smaller than skin bridges, anterior 2 organs small; mandibular canal not joined to preopercular canal with 5 pores and 4 organs. Papillate superficial neuromasts on head arranged 3-5 on snout medial to first supraorbital pore, 3-4 between

supraorbital pores and anterior nostril, 1 anteroventral to anterior nostril, 1 posterior to first infraorbital pore, 4-6 from ventral spine of lower jaw behind posterior premaxillary to top of preopercle, 5-6 from angle of subopercle to behind dorsal preopercular pore, and at least 1 on posterior lower jaw.

Dorsal and anal fins far back on body; dorsal longer than anal, dorsal origin and end before and behind those of anal, always more dorsal rays, usually 3 more, range 2-4; in undamaged specimens all but first ray of dorsal and anal branched, middle rays longest. Pectoral low, short, directed posterodorsally, middle rays longest, none branched, last 2 rays very short, apparently fused to last largest ray in largest specimens. Caudal fin rays all broken, no accurate counts of principal rays possible, fin shape unknown.

Ovaries paired, 33 dissected specimens (27.6-131 mm), all but 1 with eggs 0.1-0.15 mm diameter or less, ovaries flacid to rounded, increasing in length with age (Fig. 14); 1 specimen 112 mm with well-rounded ovaries extending forward halfway to pectoral girdle, with eggs of varying sizes from less than 0.1 mm to ca. 0.25 mm diameter, attached to internal wall and folds of ovary, none free in lumen, largest eggs with visible oil drop (Fig. 8b); only this specimen with considerable fat in abdominal cavity. Small, short, median bladder dorsoposterior to ovaries in largest specimens, indeterminate in smaller specimens. Urogenital papilla behind anus and ovarian opening, most distinct in smaller specimens. No testes apparent.

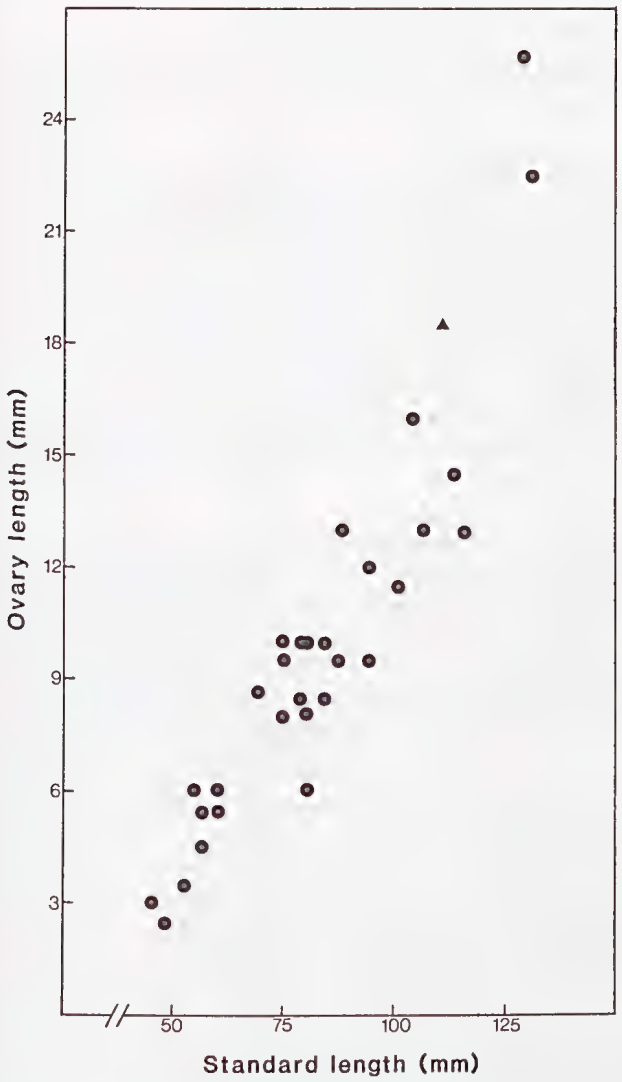

Fig.14. *Ditropichthys storeri* ovary length versus standard length; triangle indicates specimen with eggs more than 0.15 mm diameter.

Colour in alcohol very dark brown; oral and gill cavities very light brown; stomach and peritoneum dark brown, intestine without pigment.

Distribution. More than 80 specimens have been collected in all three oceans, from 41°N to 43°S in the Atlantic and from 45°N to 32°S in the Pacific (Fig. 15). The distributional gaps in the central south Atlantic, south Indian and various parts of the Pacific are presumably due to inadequate sampling. The species appears to have a circumglobal distribution between 45°N and 45°S.

The vast majority of specimens have been taken in nets fishing below 1000 m. Three specimens were taken in closing nets between 1200 and 1550 m, both day and night, and 1 specimen was taken diurnally between 900 and 1100 m; two of these specimens were only 30-40 mm SL (Fig. 16). All specimens over 90 mm were taken with nets fishing to 1550 m or deeper, while four of the six captures shallower than 1000 m (650-877 m) took specimens less than 35 mm. Larger specimens appear deeper dwelling and smaller specimens may undertake a limited vertical migration to 650 m nocturnally.

Etymology. After David Humphrey Storer, author of the 'History of the Fishes of Massachusetts'.

Type specimen. The holotype, USNM 35634, has been missing from the USNM collections since at least 1965 and is presumed lost. Although some Goode and Bean specimens were deposited at MCZ, there is no indication that this specimen was ever registered at MCZ. With such distinctive features as belly ridges and joined anal lappet flaps, there has never been a question as to the identity of the species, even though the holotype apparently has not been re-examined since the original description.

Remarks. Although considerable variation is apparent in the morphometrics of the 26 measured specimens (Table 4), most of this can be accounted for in the great size range measured (27-128 mm) and, even though relatively undamaged and undistorted specimens were used, the difficulty of accurate measurements of soft specimens. Counts of dorsal and anal rays, vertebrae, lateral line scales and gill rakers varied by counts of 5 or less and no variation in morphometrics or meristics could be correlated to indicate more than one species is represented. The extreme counts of 38 and 42 vertebrae were found in only one specimen each of 39 fish x-rayed. Ranges and means of specimens from the Pacific (n = 6), Indian (n = 1), north Atlantic (n = 11) and south Atlantic Oceans (n = 8) were compared and no differences were apparent. The most striking difference found, the elongate copular tooth plate

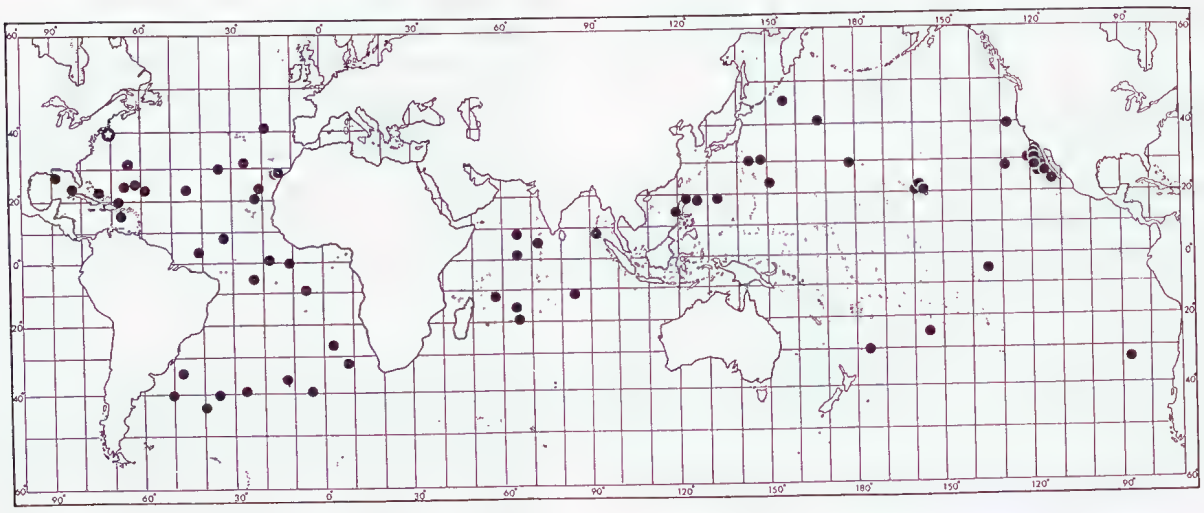

Fig.15. *Ditropichthys storeri* horizontal distribution; symbols may represent more than one specimen, star indicates holotype.

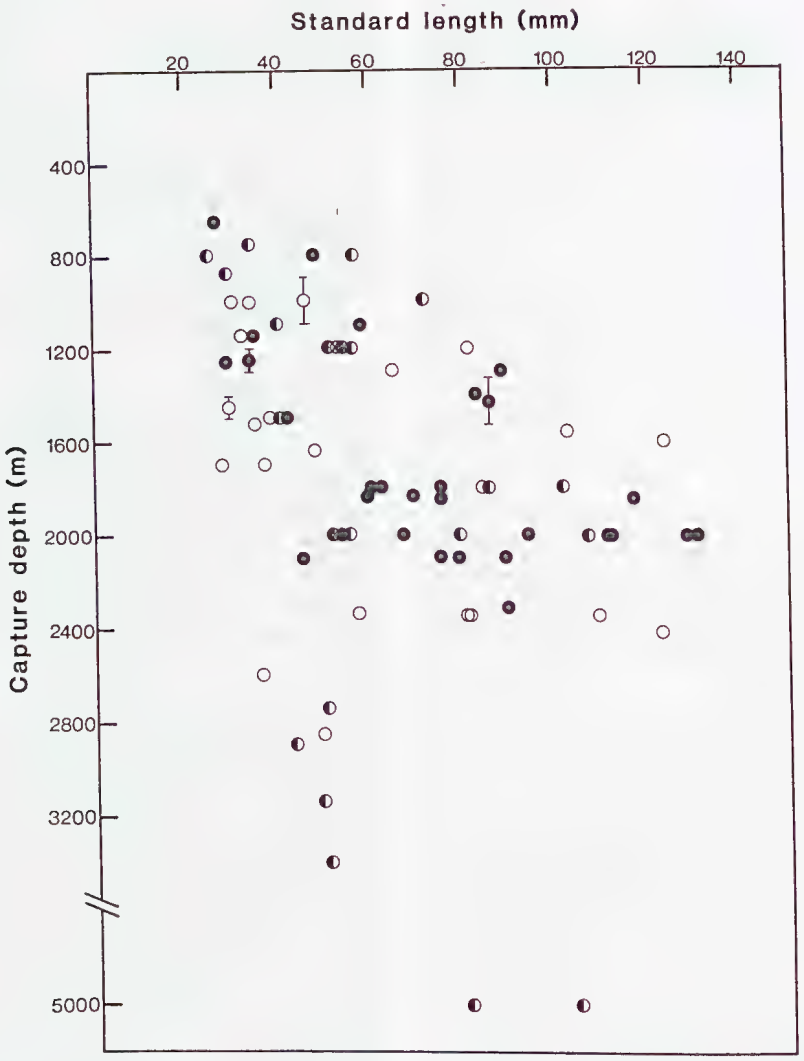

Fig.16. *Ditropichthys storeri* vertical distribution; open symbols indicate day captures, solid symbols night captures, half solid symbols day/night or unknown time, depths are maximum fishing depths of open nets; closing net captures indicated by vertical bars giving fishing depth limits.

of one northeast Pacific specimen, was not correlated with any other difference.

A comparison of morphometric values by size class (Table 4) indicates allometry in a number of features. As with most cetomimids, the eye is relatively larger in small specimens and does not appear to increase in absolute size beyond 1.1-1.3 mm in diameter, while specimens of 40 mm have eye diameters of 0.7-0.9 mm. Similar to the species of *Cetichthys*, the body fills out with flesh with increasing size; body depth and dorsal-anal distance both increase with increasing size, reflecting the tendency for larger specimens to be more robust. No other allometry is striking. The standard deviations of more than 10% of the mean for six of the 17 measurements that lack allometric growth indicate these measurements are too variable to be of great value. In particular, measurements of head, eye and posterior maxillary widths are susceptible to variation from distortion.

Cetichthys n.gen.

Type species. *Cetomimus* (*Psapharocetus*) *indagator* Rofen, 1959.

Diagnosis. *Cetichthys* differs from all other cetomimid genera in having a short ectopterygoid tooth patch, about as long as 1-2 eye diameters and ending far before the rictus, and holobranchs on all 4 gill arches very short and far separated. The lack of palatine teeth and the form of the gill arch tooth plates as short, rounded knobs are shared only with *Notocetichthys*, while the low number of vertebrae (39-43) is shared only with *Ditropichthys* and *Notocetichthys*, and the position of the anus far in front of the anal fin is shared only with *Procetichthys* and *Notocetichthys*.

Description. D. 13-16; A. 12-14; P. 19-24; principal C. 5-7+6=11-13; vertebrae 24-26+15-18=39-43; trunk canal lateral line organs and scales 8-14. Size large, maximum 196 mm; head large to very large, 2.6-3.2 in SL and moderate to wide, width at eye 2.5-5.2 in HL; snout rounded and moderate, 2.7-3.0 in HL; mouth large to very large, jaws ending slightly closer to opercular margin than eye; dorsal and anal bases short, 2.1-4.5 in HL; caudal peduncle moderate to very long, 1.3-2.0 in HL and moderate to deep, depth 2.1-4.0 in CPL; anus far from anal origin, distance 0.8-1.1 in CPD.

Nasal organ short and high without lamellae or ridges. Eye tiny, 25-47 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores; based on *C. parini* only, supraorbital canal with 6 pores joined to main canal with 2 pores, infraorbital canal with 8 pores joined to main canal with last neuromast slightly displaced anteriorly, mandibular canal with 5 pores slightly separated from preopercular canal with 5 pores; neuromasts moderate sized, papillae like, delicate. Lower jaw with weak lateral and ventral spines or projections posteriorly. Jaw teeth short to long, width 1-3 in length, closely set in indistinct diagonal rows; vomerine tooth patch triangular or diamond shaped, flat; palatine teeth absent; ectopterygoid tooth plate very short, ending far before rictus; copular tooth patch on 1 plate, short to long, 3-10 in HL, and moderate to broad, width 3.6-8.8 in length.

Free gill arches 4, with slit behind ventral arm of fourth arch; holobranchs very short and far spaced on all 4 arches, present on dorsal arm of all 4 arches. Gill rakers as round knobs with small teeth on all 4 arches, 3+1+6-9 on first arch; tooth plates present on medial face of all 4 arches; no ventral pharyngeal tooth plates.

Lateral line a broad tube pierced by very wide pores without flaps or keels; lateral line scales large, round, flat. Cavernous tissue weakly developed between anus and anal origin, none elsewhere. No subpectoral organ visible. No paired abdominal ridges or diagonal midbody ridges. A single anal lappet and ridge present or absent; no membranous curtain connecting posterior anal rays. Stomach darkly pigmented.

Etymology. From the Greek, *cetus* (*keto*) - whale and *ichthys* - fish, in reference to the body shape, mouth size and common name. The gender is masculine.

Remarks. A total of 12 specimens have been collected from 45°N to 40°S in the Pacific, in the east and west Indian Ocean and in the Atlantic at 37°S (Fig. 11). Two species are represented.

Key to the Species of *Cetichthys*

1. Lateral line scales 12-14, pores 13-15; anterior 5-7 lateral line pores equal to or smaller than width of scales; caudal peduncle length 4-4.5 in SL; anal base length 10-11 in SL; no anal lappet or ridge at anterior anal base.....*C. indagator*

------ Lateral line scales 8-10, pores 9-11; anterior 5-7 lateral line pores wider than width of scales; caudal peduncle length 5-6 in SL; anal base length 7-8.5 in SL; 1 small anal lappet without scale at end of weak ridge at base of anal ray 3.....*C. parini*

Cetichthys indagator (Rofen, 1959)

Figs 11, 12, 17

Cetomimus (*Psapharocetus*) *indagator* Rofen, 1959: 255, fig. 1. Holotype: ZMUC P23451, *Galathea* Stn 186 from the east coast of South Africa, 32°33'S, 32°01'E, 3620 m, 1645 hrs, 31 Jan. 1951.

Cetomimus indagator.-Smith, 1961: 566 (South African specimen listed).-Nielsen, 1974: 44 (holotype listed).-Paxton & Bray, 1986:433, fig. 135.1 (redescription).

Material examined. 4(51.5-128.8): ISH 1186/71, 128.8 mm SL, 37°08'S, 5°23'E, South Atlantic Ocean, 0-2200 m, N, 21 Mar. 1971; ZMUC P23451(holotype) , 117.7 mm SL, 32°33'S, 32°01'E, South Indian Ocean, 0-3620 m, D, 31 Jan. 1951; LACM 11314-1, 92.5 mm SL, 40°07'S, 161°08'E, South Pacific Ocean, 0-3150 m, DN, 4 Dec. 1966; NSMT(from ORI) P44368, 51.5 mm SL, 20°03'N, 130°05'E, North Pacific Ocean, 0-ca.1750 m, D, 20 Jan. 1985.

Diagnosis. See *C. parini* diagnosis.

Description. The holotype is in reasonable condition, with most of the skin of the lateral line and head canals torn or missing. The ISH specimen is in very poor condition with head and abdomen torn open and the pectoral fins and about one quarter of the skin gone. The LACM specimen is in reasonable condition, but totally faded, without colour. The NSMT specimen is very poor, with smashed head and lost skin.

D. 14-15; A. 12-13; P. 21; principal C. 6-7+6; procurrent C. 5+7; vertebrae 24+17-18=42-43; trunk canal lateral line scales/organs 12-14. Measurements in Appendix Table 5.

Body oval in cross section, greatest depth at level of pectoral base. Caudal peduncle much longer than deep, depth 2.7-4.0 in length. Anus far from anal fin origin, distance about equal to caudal peduncle depth. Cavernous tissue weakly developed anterior to anal fin origin, not reaching anus or ventral midline, most prominent in smallest specimen. Mid-dorsal and midventral keels not apparent. No anal lappet flaps, scales or ridges at base of anal fin. No subpectoral organ visible.

Head very large, compressed, much deeper than wide; in smallest specimen anterior head depressed and concave; head and anterior body profile weakly rounded. Nostrils similar to lateral line head pores, torn in all specimens, closer to tip of snout than eyes; raphe short and high without lamellae, ridges or pigment. Eye small, without lens, about midway between upper profile of head and upper jaw. Interorbital broad and convex; posterodorsal projections above eye most prominent in smaller specimens.

Mouth enormous, slightly oblique; jaws slightly concave; rictus 1-2 eye diameters before posterior end of premaxilla; posterior end of jaws well before edge of gill cover; lower jaw with weakly developed lateral and ventral spines posteriorly, more prominent in smaller specimens. Jaw teeth small, very long in inner row with length more than 3 times width, decreasing to outer row of very short teeth, all depressible orally; teeth closely set in irregular rows, without posterior clumping or grouping; premaxilla with 3 anterior and 3-4 posterior irregular rows, total number of teeth in approximate row 65-130; dentary with 3-4 anterior and 4-9 posterior irregular rows, total number of teeth in approximate row 55-130, numbers and rows increasing with size; dentary teeth extending 1 eye diameter or less behind rictus. Vomerine teeth short, in 1-5 rows forming roughly oval-shaped patch of 7-23 total teeth, numbers increasing with size; no palatine teeth; ectopterygoid tooth patch short, about 1.5 eye diameters long and under or slightly behind eye, teeth short to medium in 2 rows with 12-23 teeth in longest row. Copular tooth plate moderate in length and width, length 4.1-11.7% SL decreasing with increasing size, club shaped with posterior end largest and rounded, anterior pointed; teeth short, in irregular rows, about 3-6 rows across narrowest point and 27-38 rows along length.

Free gill arches 4, with moderate slit behind ventral arm of fourth arch; dorsal arms of first 3 arches free, fourth bound in skin of gill chamber. Holobranchs of all 4 arches poorly developed, short and far spaced, those of first arch about 3-4 in width of bony arch, filaments of fourth arch about twice length of those of first arch; separate holobranchs on ventral arm of first arch 27-32, on ventral arm of fourth arch 13-24; holobranchs present on dorsal arm of all 4 arches. Normal gill rakers absent; short, raised,

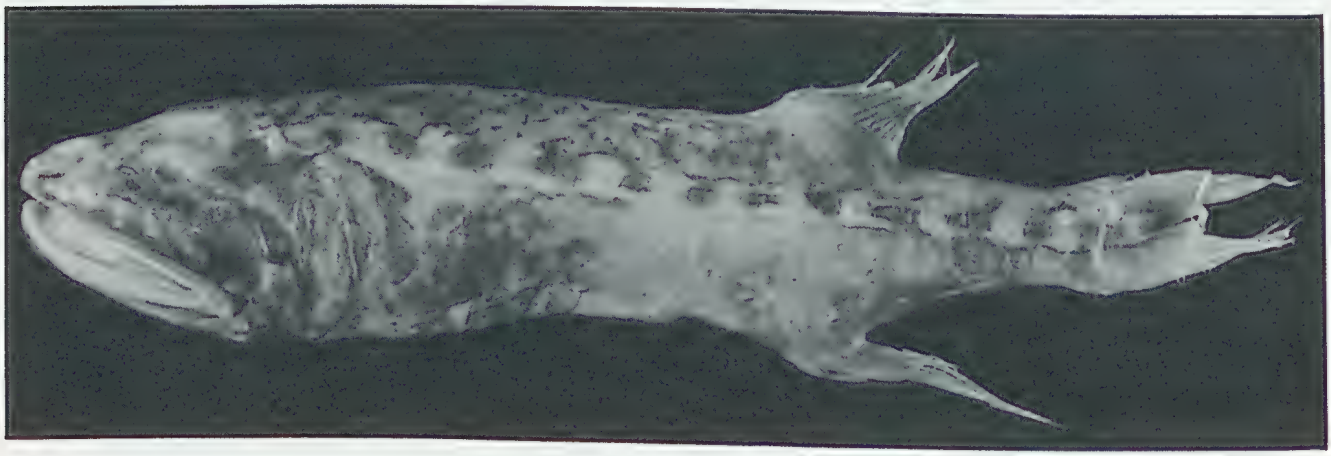

Fig.17. *Cetichthys indagator* holotype, 117.7 mm, ZMUC P23451; photo J. Fields, AMS.

rounded knobs covered with tiny, depressible teeth on all 4 arches, those in angle elongate and almost club shaped; gill knobs of first arch 3+1+8-9, of fourth arch 1-2+1+5-6; smaller raised tooth plates on medial faces of ventral arms of all 4 arches, numbering 8-9, 7-9, 6-8, 3-5. Dorsal pharyngeals as pair of small, high-crowned tooth plates, anterior plate kidney to oval shaped, much larger than posterior; posterior plate oval shaped; both plates covered with small, depressible teeth much larger than those on gill knobs. No ventral pharyngeal tooth plates.

Lateral line a broad, shallow tube of thin, fragile overlying skin with 13-15 wide pores without flaps or keels; 12-14 underlying scales, round, flat, without projections, interspaces half to 1 scale width between first 5-7 scales, wider than scales posteriorly; skin bridges over organs narrower than scales, usually lost; 1-2 papillae on remaining skin bridges; 2 papillae at bases of middle caudal rays behind last lateral line pore in ISH specimen; 1-2 papillae in dorsal midline behind head, presumed remnants of 2 lost rows of dorsal accessory line of superficial neuromasts.

Lateral line system of head with shallow canals and wide pores; skin bridges over neuromasts forming pores mostly torn; no complete pore/organ counts or superficial neuromast counts possible on any specimen; few remnants present indicate similarity to *Cetichthys parini*. Skin smooth, thin, fragile, lacking scales except in lateral line.

Dorsal and anal fins far back on body; dorsal origin distinctly before anal; dorsal base longer than anal, ending behind anal; anal base non symmetrical, origin elevated on extension of body behind anus; last anal ray base under 2nd or 3rd penultimate dorsal ray; dorsal and anal rays 6-10 longest, none branched. Pectoral fin low, short, directed posteriorly, upper rays longest, none branched. Caudal fin weakly emarginate to rounded, no rays complete.

Ovaries of 2 largest specimens paired, orangish, about 15 mm long, flaccid, with very tiny eggs; bladders paired, about one third length of ovaries in holotype, whitish, as long as ovaries in LACM specimen but hollow and balloon like, without apparent internal structure. No obvious urogenital papilla, urogenital opening immediately behind anus in holotype, perhaps in area before anal fin origin in LACM and ORI specimens.

Colour in alcohol light to dark brown; oral and gill cavities without pigment; stomach and peritoneum dark brown, intestine without pigment. Colour of LACM specimen when freshly caught brown with red-orange on head and dorsally, red-orange in oral and gill cavities.

Distribution. The three larger specimens were taken in the southern hemisphere between 30°-40°S, one in each ocean, and the smallest in the north-west Pacific (Fig. 11).

The three larger specimens were taken in open nets fishing to at least 2200 m, the smallest specimen in an open net with 5000 m of wire out, perhaps fishing to between 1500-2000 m (Fig. 12).

Etymology. From the Latin *indagator* - explorer.

Type specimen. The holotype of *C. indagator*, ZMUC P23451, was re-examined and appears to have an abnormaly shortened anal fin base (Fig. 17).

Remarks. The original description of *C. indagator* is detailed, but some interpretations require emmendation. The only teeth in the roof of the mouth other than those on the vomer are located far behind the vomer under the level of the eye; these are ectopterygoid rather than palatine teeth. The species of *Cetichthys* and *Notocetichthys* are the only cetomimids to lack teeth on the palatine, which is located immediately posterolateral to the vomer and extends posteriorly to the ectopterygoid. Rofen (1959:256) and Harry (1952:63,65) refer to the ectopterygoid teeth of other species of cetomimids as the posterior palatine patch. Rofen (1959:256) described the gill rakers of *C. indagator* as "... small round bony plates covered with gill teeth ...". These structures are not plates, but raised knobs (Fig. 3b) that most closely approach the club-shaped gill rakers of *Ditropichthys* and are unique to species of *Cetichthys* and *Notocetichthys*.

The identification of the small, smashed specimen from south of Japan was somewhat equivocal, but the long caudal peduncle, higher vertebral number and shorter anal fin base were considered decisive.

The dentition of the smallest specimen is prominent, with the individual teeth relatively longer than those of the larger specimens. The length of the copular tooth patch is striking, 11.7% SL, and displays allometric growth in the larger specimens, decreasing to 4.1% SL in the largest; the absolute length of the tooth patch remains constant or even decreases with size, ranging from 6.0-5.2 mm. The other feature that displays allometric growth is eye diameter, with an absolute measurement of 1.0-1.2 mm in all four specimens.

Cetichthys parini n.sp.

Figs 1g, 2b, 3b, 4c, 11, 12, 18

?*Cetomimus* sp.-Stein, 1985: 190 (in part, California specimens listed).

Type material. HOLOTYPE: SIO 53-344, 196.2 mm, Transpac 44/65, north-west Pacific south-east of Kurile-Kamchatka Trench, 45°24'N, 154°11'E, 0-ca.4680 m, 1245-2138 hrs, 16 Sept. 1953.

PARATYPES: 7(87.5-174 mm): OSUO 2552-3, 2(121.6-174 mm), *Golden Fleece* 2499/4, north-east Pacific off California, 39°23'N, 127°57'W, 2900-3000 m, closing net, 2127-0027 hrs, 10 Dec. 1981; SIO 87-9, 157.2 mm, Atom KLS141F, north-east Pacific off California, 32°50'N, 124°7'W, 2700 m, closing net, 28 May 1986; ZIN 47877, 104.2 mm, *Vityaz* 5082, central Pacific, 5°58'N, 139°57'W, 0-ca. 5000 m, 1320-1655 hrs, 16 Sept. 1961; AMS I.27258-001 (from ZIN 47875), 96.0 mm, *Vityaz* 3503, west Pacific, 23°05'N, 144°54'E, 0-ca.7000 m, 14 Oct. 1955; NSMT P60001 (from TH 800403), 88.6 mm, *Kaiyo Maru* Kocnet 9A, north-west Pacific off Bonin Island, Japan, 31°05'N, 147°35'E, 2887-3329 m, closing net, 2000-0800 hrs at depth, 27-28 May 1980; ZIN 47876,

87.5 mm, *Vityaz* 4535, east Indian Ocean off Bali, Indonesia, 10°04'S, 108°E, 0-ca.5800 m, 4 Nov. 1959.

Diagnosis. *Cetichthys parini* differs from *C. indagator*, its only congenor, in having fewer trunk canal lateral line scales and organs (8-9 versus 12-14) and pores (9-10 versus 13-15), vertebrae (39-41 versus 42-43), gill knobs on the ventral arm of the first (7-8, rarely 9 versus 9-10) and fourth (4-6 versus 6-7) gill arches, shorter caudal peduncle (16.7-19.2 versus 24.1-24.7% SL) and longer anal fin base (11.5-14.3 versus 7.1-9.9% SL). In addition *C. parini* has the anterior 5-7 scales of the lateral line further apart, with the interspaces wider than 1 scale width (versus anterior 5-7 interspaces equal to or less than one scale width), a weakly developed anal lappet without a scale at the anterior anal base (versus absent), the copular tooth patch longer and narrower than in specimens of *C. indagator* of similar size and the teeth of the posterior dentary and especially premaxillary grouped into clumps, particularly in specimens less than 130 mm (versus no clumping of posterior jaw teeth).

Description. The holotype is in good condition, although the skin of the lateral line and head canals is torn or missing and the fins are incomplete. The larger OSUO paratype is poor, with a badly smashed head; the smaller OSUO and SIO paratypes are in good condition, with only some of the lateral line missing. All of the ZIN paratypes are in good condition, except for broken jaws, but the NSMT paratype has lost about half the skin. The values of the holotype are followed by the range of values of the paratypes in brackets.

D. 14(13-16); A. 13(12-14); P. ?(19-24); principal C. ?(5-6+6); procurrent C. ?(4-5+4-5); vertebrae 24+15 =39 (24-26+15-17=40-41); trunk canal lateral line scales and organs 8(8-9). Measurements in Appendix Table 5.

Body oval in cross section, greatest depth at level of pectoral base. Caudal peduncle longer than deep, depth 2.1-3.6 in length. Anus far from anal fin origin, distance about equal to caudal peduncle depth. Cavernous tissue weakly developed with little structure, most prominent in smallest specimens, just anterior to anal fin origin, not reaching anus or ventral midline. Low but distinct mid-dorsal and midventral keels in most specimens extending anteriorly from dorsal origin and anus respectively. One anal lappet flap without scale at base of anal ray 3 set at end of very low ridge from anal ray 1 (Fig. 18b). No subpectoral organ visible.

Head very large, slightly compressed and distinctly deeper than wide; in smaller paratypes head anteriorly depressed and strongly concave from jaws to dorsal midline; head and anterior body profile weakly rounded with uneven pits and projections on top of head, bony projections posterodorsal to eyes prominent in smaller paratypes. Nostrils similar to head lateral line pores, torn in all specimens, closer to tip of snout than eyes; raphe short, high, without lamellae or ridges, situated below anterior nostril, weakly pigmented basally in some specimens (Fig. 1g). Eye small, without lens even in smallest specimens, nearer upper profile of head than upper jaw. Interorbital very broad, weakly convex.

Mouth enormous, slightly to moderately oblique; jaws slightly to moderately concave; rictus 2-3 eye diameters before posterior end of premaxilla; posterior end of jaws well before end of gill cover; lower jaw with weakly developed lateral and ventral spines posteriorly, more prominent in smaller paratypes. Jaw teeth small, more elongate in inner row with length sometimes more than 3 times width, decreasing to outer row of very short teeth, all depressible (Fig. 1b); teeth in irregular rows with distinct

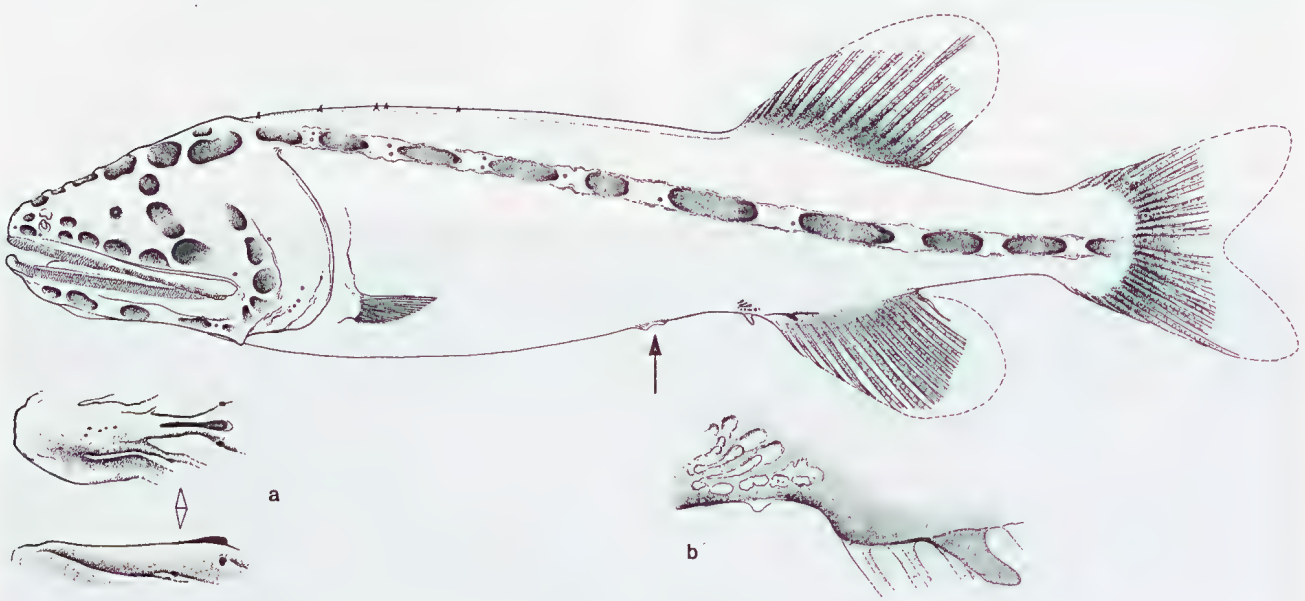

Fig.18. *Cetichthys parini* holotype, 196.2 mm, SIO 53-344, arrow indicates level of anus; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, *C. parini* paratype, 87.5 mm, ZIN 47876, showing cavernous tissue and anal lappet, right hand side.

grouping into clumps in posterior jaws of smaller specimens, not as distinct in holotype; premaxilla with up to ?(3-4) anterior and 4(4-6) posterior irregular rows, total number of teeth in approximate row ?(105-145, 3 specimens counted); dentary with up to 5(4-5) anterior and 9(7-8) posterior irregular rows, total number of teeth in approximate row 171/178(95-165, 4 specimens), tooth numbers and rows increasing with specimen size; teeth on dentary extending about 1-1.5 eye diameters behind rictus. Vomerine teeth short, in 3(1-4) rows usually forming an approximate oval-shaped patch totalling 13(9-20) teeth, number not correlated with size; no palatine teeth; ectopterygoid tooth patch short, about 1-2 eye diameters in length, under or slightly behind eye, teeth short to medium, in 2(2-4) rows with 24(13-22) teeth in longest row. Copular tooth plate moderate in length and slender, length 3.5 (4.4-8.9)% SL, decreasing with increasing size, club shaped with posterior end largest and rounded, anterior end pointed (Fig. 18a); teeth short, in irregular rows, about 4(2-5) rows across narrowest point and 32(32-51) rows along length.

Free gill arches 4, with moderate slit behind ventral arm of fourth arch; dorsal arms of first 3 arches free, fourth bound in skin of oesophagus. Holobranchs of all 4 arches poorly developed, short and far spaced, those of first arch about 3-4 times in width of bony arch (Fig. 3b); holobranchs of fourth arch about 2 times length of those of first arch; separate holobranchs on ventral arm of first arch 32(27-32), on ventral arm of fourth arch 20(16-21); holobranchs present on dorsal arm of all 4 arches. Normal gill rakers absent; short, raised, rounded knobs covered with tiny depressible teeth on all 4 arches, those in angle elongate and almost club shaped; gill knobs of first arch 3+8(7-9), of fourth arch 2(1-2)+6(4-6); smaller raised tooth plates on medial faces of ventral arms of arches 1-4, numbering 7(5-8), 7(5-6), 6(3-5), and 2(2-3). Dorsal pharyngeals as pair of small, high-crowned tooth plates, anterior plate kidney to oval shaped, distinctly larger than posterior; posterior plate tear-drop, kidney or oval shaped, somewhat pointed medially in some specimens; both plates covered with small, depressible teeth much larger than teeth on gill knobs. No ventral pharyngeal tooth plates.

Lateral line a broad tube, moderately deep in holotype, shallow in paratypes, of thin overlying skin with 9-10 wide pores without flaps or keels; 8-9 underlying scales, round, flat, without projections, interspaces wider than scale width; skin bridges over neuromasts narrower than scales, usually lost; 1-6 papillate neuromasts on some remaining skin bridges; 2-3 papillae at bases of caudal rays behind and above last lateral line pore; dorsal accessory line of superficial neuromasts as 2 mid-dorsal rows of widely-spaced papillae from level of top of gill opening posterior to about halfway to dorsal fin origin, rows close together posteriorly, divergent anteriorly, about 6-8 papillae per row.

Lateral line system of head with cavernous canals in holotype, shallow canals in paratypes, and wide pores (Fig. 4c); skin bridges over neuromasts forming pores mostly complete in holotype, torn in paratypes. Supraorbital canal with 6 pores and 5 neuromasts joined to main canal with 2 pores and 3 neuromasts (last before top of gill slit), with supratemporal pore and neuromast medial to pore 2. Infraorbital canal with 8 pores and 6 lower and 2 upper neuromasts, joined to main canal at 1st pore, last 2 neuromasts and associated pores slightly displaced anterodorsally. Mandibular canal with 5 pores and 4 neuromasts, almost joined to preopercular canal with 5 pores and 4 neuromasts. Papillate superficial neuromasts on head mostly lost?, 1-2 on snout, 1-2 below nostrils, 1 above posterior tip of premaxillary, 1 behind uppermost preopercular organ, 3-4 just above angle of preopercle, at least 2 over last lower jaw pore. Skin smooth, lacking scales except in lateral line, that of holotype thicker, of paratypes thin and fragile.

Dorsal and anal fins far back on body; dorsal origin slightly before anal origin; ends of dorsal and anal opposite; fin rays incomplete. Pectoral fin low, short, directed posteriorly, upper rays longest. Caudal fin weakly to moderately forked in specimens with complete rays.

Ovaries paired, orangish in 2 largest specimens with eggs less than 0.1 mm, increasing in size with age. Bladders paired, whitish and covered with light layer of pigment, rounded with small lobes in largest specimens, attached to dorsal mesentary before end of ovary, 9.5 mm by 3 mm in holotype, much smaller in all others. None of the specimens with fully developed ovaries and presumably all are juveniles. Much of abdominal cavity filled with fat in two largest specimens. Four smallest paratypes with distinct urogenital papillae just before anal fin origin under level of cavernous tissue; no papillae apparent in four largest specimens, urogenital opening just behind anus in holotype. Paired small, dark brown structures in body wall either side of anus visible in most specimens including holotype.

Colour in alcohol light to dark brown; oral and gill cavities without pigment; stomach and peritoneum dark brown, intestine without pigment.

Distribution. The eight specimens range from the eastern Indian Ocean and central Pacific to both sides of the north Pacific (Fig. 11).

The species is apparently the deepest dwelling of all whalefishes. Four captures were made with closing nets, all fishing between 2700 and 3330 m; all other captures were made by open nets fishing to at least 4500 m (Fig. 12). It is perhaps surprising that we have so many specimens of this bathypelagic species.

Etymology. After Nikolai V. Parin, who provided the IOANM (now ZIN) collection of cetomimids for study, in recognition of his contributions to pelagic and deep sea ichthyology.

Remarks. There seems little doubt that *Cetichthys parini* and *C. indagator* are distinct species, with non-overlapping values in meristics (vertebrae and lateral line scales/organs and pores) and morphometrics (caudal peduncle length and anal fin base length (Table 5). One weak anal lappet and curved sections of posterior jaw teeth are both restricted to *C. parini* (versus absent in

C. indagator). There is also a tendency for *C. indagator* to have a higher number of tooth knobs and medial tooth plates on the gill arches and a shorter head and wider caudal peduncle, but the ranges of values overlap in the two species.

Variation within the eight type specimens of *C. parini* is considerable. The most striking difference involves the amount of flesh on the specimens, with the largest, the holotype, appearing heavy and well rounded; flesh on the head reduces the prominence of bony projections, the belly and caudal peduncle are well rounded, and a large amount of fat is present in the abdominal cavity. The largest paratype is also relatively heavy and well-filled out. In contrast the five smaller paratypes, all at least 30% shorter than the largest paratype, appear emaciated, with the head strongly convex between the upper jaw and the dorsal profile, with prominent projections, and the body slender. These differences result in the size-correlated differences of measurements of body depth and caudal peduncle depth (Table 5), that could be a function of gaining condition and laying down fat and muscle with increasing size. Allometric growth is indicated for head length, premaxillary and dentary lengths and snout to pectoral distance, all of which are greater in smaller specimens. Neither the eye diameter nor length of the copular tooth patch appear to increase in size with specimen growth; eye diameter is 1.0-1.2 mm in all specimens, while the copular tooth plate ranges from 6.8-7.9 mm, at least 0.8 mm longer than the absolute measurements of the specimens of *C. indagator*. The increased amount of tissue in the two largest specimens is also correlated with deeper canals of the lateral line system, both on the head and body.

Notocetichthys Balushkin, Fedorov & Paxton, 1989

Notocetichthys Balushkin, Fedorov & Paxton, 1989: 155. Type species *Notocetichthys trunovi* Balushkin, Fedorov & Paxton, 1989 by original designation.

Diagnosis. *Notocetichthys* differs from all other cetomimid genera in lacking vomerine and ectopterygoid teeth, in having the copular tooth patch reduced to a tiny plate behind the level of the eye, cavernous tissue in an area behind the anus with a distinct free posterior margin and prolonged posterior extension as a free, thin flap without any supporting scale, and in having 5-7 diagonal skin ridges along the midbody with each ridge centred on a lateral line scale. *Notocetichthys* is most similar to *Cetichthys*, each lacking palatine teeth and having gill arch tooth plates on short, rounded knobs. The two genera differ in the unique characters described above, and also in the condition of the infraorbital canal (joined to the supraorbital in *Cetichthys*, separate in *Notocetichthys*) and in the number of dorsal and mandibular canal pores (10 and 6-7 in *Notocetichthys* versus 8 and 5).

Description. D. 13; A. 11-13; P. 17?-19; principal C. 5-6+5-6=10-12; vertebrae 24-26+15=39-41; trunk canal lateral line scales and organs 15-16. Size moderate, maximum 109 mm; head large, 3.1-3.2 in SL and moderate to wide, width at eye 3.1-4.2 in HL; snout rounded and moderate in length, 2.5-2.9 in HL; mouth large, jaws ending about midway between level of eye and opercular margin; dorsal and anal fin bases short, 2.7-3.2 in HL; caudal peduncle moderate to long, 1.6-1.7 in HL and deep, 2.2-2.4 in length; anus far from anal origin, distance 0.8-1.0 in CPD.

Nasal organ short and broad with few weak ridges present or absent. Eye tiny, 22-32 in HL, without discernible lens. Lateral line system of head as series of wide canals with apparently large pores (skin damaged), with the following pore counts based on presence of neuromasts: supraorbital canal with 6 pores, apparently joined to main canal with 4 pores, infraorbital canal apparently separate from dorsal canal with 8 pores, last displaced anteriorly, mandibular canal with 6-7 pores, apparently joined to preopercular canal with 5 pores. Lower jaw with apparently weak lateral and ventral spines posteriorly (spines broken). Jaw teeth tiny, height less than 2 times basal width, closely set in indistinct diagonal to vertical rows; vomerine, palatine and ectopterygoid teeth absent; copular tooth patch on 1 plate, tiny, length 29-35 in HL, and relatively broad, width 1.1-2.4 in length, origin behind level of eye.

Free gill arches 4, with slit behind ventral arm of fourth arch; holobranchs long and moderately spaced on all 4 arches, present on dorsal arms of all 4 arches. Gill rakers as round knobs with small teeth on all 4 arches, 2+1+7 on first arch; tooth plates present on medial faces of all 4 arches; no ventral pharyngeal tooth plates.

Lateral line a shallow, broad tube, with wide pores; lateral line scales large, flat and round (first and last scales semirectangular). Cavernous tissue in small well-defined area behind anus with raised, free posterior margin and elongate flap without supporting scale over about third anal ray. Diagonal midbody skin ridges centred on lateral line scales 7-13. No subpectoral organ visible. No paired abdominal ridges. No series of anal lappets with scales, or ridges or membranous curtain associated with anal fin. Stomach pigment brown.

Etymology. From the Greek *noto* - southern, *cetus* (*ketos*) - whale and *ichthys* - fish, in reference to the Antarctic occurrence of the two known specimens.

Remarks. Only two specimens have been collected, in Antarctic waters at 65°S, by nets fishing to a maximum of 1275 and 1360 m depth.

Notocetichthys trunovi Balushkin, Fedorov & Paxton, 1989

Figs 11, 12, 19

Ditropichthys sp.-Trunov, 1985:296, 305 (listed from Lazarev Sea).
Notocetichthys trunovi Balushkin, Fedorov & Paxton,

1989: 156, fig. 1. Holotype ZIN 47696, 107.5 mm, FRV *Volny Veter* Stn 14, Lazarev Sea, Antarctica, 65°20'S, 02°34'E, 0-1360 m over 1370-1400 m bottom, 20 Jan. 1983; paratype ZIN 47697, 109.0 mm, FRV *Volny Veter* Stn 11, Lazarev Sea, Antarctica, 65°17'S, 2°42'E, 0-1275 m over 1285-1300 m bottom, 17 Jan. 1983.

Diagnosis. As for genus.

Description. The two type specimens are in reasonable condition, except most of the skin over the lateral line and head canals is missing.

D. 13; A. 11-13; P. 17?-19; principal C. 5-6+5-6=10-12; vertebrae 24-26+15=39-41; trunk canal lateral line scales and organs 15-16. Measurements in Appendix Table 6.

Body oval anteriorly, greatest depth at level of pectoral base. Caudal peduncle 2.2-2.4 times longer than deep. Anus far from anal origin, distance about equal to caudal peduncle depth. Cavernous tissue well developed in small, diffuse area behind anus extending to level of first anterior anal rays, with posterior edge of area raised and free and with thin, flap-like extension over anal fin similar to very narrow anal lappet but without supporting scale. Low, narrow, diagonal ridges of skin centred on 6-7 lateral line scales from before to behind dorsal fin; ridges expand at lateral line to form skinbridge over neuromast; white vessels inside ridges that expand at ends of ridges to form networks of tiny vessels under dorsal and anal bases and over caudal peduncle. No mid-dorsal or midventral keels apparent. No anal lappet flaps, scales or ridges over anal fin base.

Head very large, deeper than wide with almost straight profile from snout to occiput. Nostrils closer to tip of snout than eye, round, anterior about twice diameter of posterior, skin bridge about as wide as posterior nostril; nasal organ short and broad with few weak ridges present in one specimen, situated below anterior nostril, covered by light brown pigment. Eye small, without discernible lens, closer to top of head than upper jaw.

Mouth large, slightly oblique; rictus 1-2 eye diameters before end of premaxillary; posterior end of jaws closer to level of eye than margin of operculum. Jaw teeth tiny, triangular, height less than 2 times basal width, closely set in indistinct diagonal to vertical rows, depressible orally. No vomerine, palatine or ectopterygoid teeth. Copular tooth plate tiny, 0.9-1.1% SL, on posterior copula about midway between levels of eye and posterior premaxilla, oval to rectangular, width 1.1-2.4 in length, with about 18 tiny teeth set in approximately 3 rows, middle row longest.

Free gill arches 4, with moderate slit behind ventral arm of fourth arch; dorsal arms of first 3 arches free, fourth bound in skin of gill chamber. Holobranchs of all 4 arches moderately long and moderately spaced, those of first arch about four fifths as long as bony width of arch; holobranchs of fourth arch about equal to or slightly longer than those of first arch; holobranchs present on dorsal arms of all 4 arches. Normal gill rakers absent; short, raised, rounded knobs covered with tiny teeth on all 4 arches, those in angle elongate and almost club shaped; gill knobs of first arch 2+7-8, second arch 1+8, third arch 1+4, fourth arch 1+6; smaller raised tooth plates on medial faces of ventral arms of all 4 arches, numbering 7, 7, 5, and 4 respectively (only 1 specimen counted). Dorsal pharyngeals as 2 pair of small, high-crowned tooth plates, directed medially rather than ventrally so that anterior plate of right side abuts between anterior and posterior plates of left side; plates roughly dome shaped, posterior half to two thirds size of anterior, both covered with about 4 rows of teeth similar in size and shape to jaw teeth. No ventral pharyngeal tooth plates.

Lateral line a broad, shallow tube with overlying skin mostly lost, anterior skin bridges apparently very narrow;

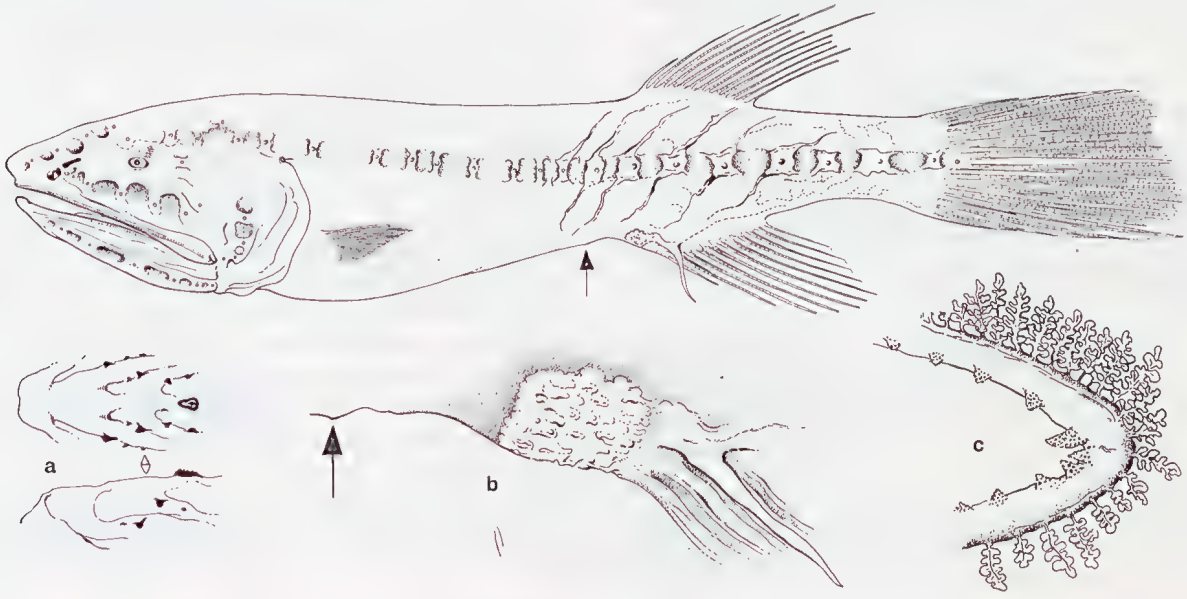

Fig.19. *Notocetichthys trunovi* holotype, 107.5 mm, ZIN 47696, arrow indicates level of anus, dashed lines indicate white "veins"; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, enlargement of cavernous tissue; c, first gill arch, left side (not to scale).

anterior pores almost round, posterior pores longer than wide; 15-16 lateral line scales round and flat (first and last semirectangular) without projections; some anterior scales close together; others wide apart, interspaces as wide as scale posteriorly; no papillate neuromasts observed on lateral line or mid-dorsally; 2 papillae on basal quarter of caudal fin.

Lateral line system of head with wide, shallow canals and moderate to large neuromasts, overlying skin mostly lost. Supraorbital canal with 6 pores and 5 neuromasts, apparently joined to main canal with 4 pores and neuromasts, supratemporal medial to pore 3. Infraorbital canal with 8 pores and 7 neuromasts, the last slightly displaced anterodorsally behind eye, apparently separate from main canal. Mandibular canal with 6-7 pores and 5-6 neuromasts, joined to preopercular canal with 5 pores and 4 neuromasts. No distinguishable papillae on head. Skin smooth, thin and fragile, without scales except in lateral line.

Dorsal and anal fins far back on body; dorsal origin slightly to distinctly before anal origin; both fins exceptionally long rayed, longer than any other cetomimid; middle dorsal and anal rays longest, none branched. Pectoral fin moderately high on body, short, directed dorsoposteriorly; upper 5-6 pectoral rays longest, none branched. Caudal fin weakly forked to emarginate.

Ovaries paired, organish, about 9 mm long in paratype, with tiny eggs less than 0.1 mm diameter. Bladders paired, very thin walled without apparent internal structure, almost as long as ovaries, and about half as wide as long. Possible urogential papilla just before anal fin origin, far behind anus.

In life claret coloured, tips of fins bright orange, belly with bluish tinge, mouth and gill cavities pink (Baleshkin *et al.*, 1989). Colour in alcohol moderate brown to grey brown; oral cavity without pigment, except brown skin flap medial to teeth, gill cavity light brown; peritoneum dark brown, stomach moderate brown, intestine without pigment.

Distribution. The only two specimens come from bathypelagic waters of the Antarctic (Fig. 11). The only other cetomimids known from such southern waters are two species of the genus *Gyrinomimus* (Fedorov & Balushkin, 1983; Fedorov, Balushkin & Trunov, 1987).

Both specimens were collected between the surface and 1400 m (Fig. 12). It is noteworthy that both were caught in pelagic nets fishing less than 100 m off the bottom, indicating that perhaps this species is benthopelagic.

Etymology. After I.A. Trunov of the Atlantic Fisheries and Oceanographic Research Institute, Kaliningrad, who collected the two type specimens.

Remarks. The holotype of *Notocetichthys trunovi* was taken in the same haul as the holotype of *Gyrinomimus andriashevi* (Balushkin *et al.*, 1989).

Danacetichthys n.gen.

Type species. *Danacetichthys galathenus* n.sp.

Diagnosis. This new genus has small, elongate teeth closely set in well-defined longitudinal rows in the jaws and palate, unlike all other cetomimid genera except *Gyrinomimus*. *Danacetichthys* differs from *Gyrinomimus* in the presence of ventral pharyngeal tooth plates on the fifth ceratobranchial, number of free gill arches (4 versus 3), vertebral number (43-46 versus 47-59), shape of lateral line scales (round or widely rectangular and flat versus strap like or narrowly rectangular and curved) and maximum size (54 mm versus 390 mm).

Description. D. 14-16; A. 14-15; P. 21-23; principal C. 13-15?; vertebrae 26-29+15-20=43-46; trunk canal lateral line organs and scales 16-18. Size small, maximum known 54 mm; head very large, 2.7-2.8 in SL and wide, width at eye 2.6-3.8 in HL; snout rounded and moderate, 2.9-3.3 in HL; mouth very large, jaws ending much closer to opercular margin than level of eye; dorsal and anal bases short to moderate, 2.0-3.2 in HL; caudal peduncle short to moderate, 2.0-3.8 in HL, and moderate to deep, 1.3-2.3 in CPL; anus close to anal fin, distance 2.6-6.3 in CPD.

Nasal organ small and low, without lamellae or ridges. Eye small, 15-19 in HL, but with lens well developed or reduced. Lateral line system of head a series of large canals with wide pores, no canals undamaged; supraorbital canal with 6 pores, apparent break between last supraorbital and first main canal pore, main canal with 3-4 pores, infraorbital canal with about 9 pores, the last displaced, not joined to main canal, mandibular canal about 8 pores, unknown if joined to preopercle with about 4 pores; neuromasts tiny and delicate. Lower jaw with weakly developed lateral and ventral spines posteriorly. Jaw teeth elongate, inner row with length more than 3 times basal width, closely set in well defined longitudinal rows; vomerine tooth patch rectangular, ellipsoidal or triangular; palatine and ectopterygoid teeth distinct, latter reaching level of rictus; copular tooth patch short to moderate and broad.

Free gill arches 4 with slit behind ventral arm of fourth arch; holobranchs well developed on all 4 arches; holobranchs on dorsal arm of first arch. Gill rakers as separate, slightly raised, round or ellipsoidal patches of small teeth on all 4 arches (9-10 on first arch), but none on medial faces; ventral pharyngeal tooth plates present.

Lateral line a broad, thin-walled tube pierced by very wide pores; lateral line scales round or widely rectangular, posteriorly close together. Cavernous tissue only at anus. Subpectoral organ present. No paired abdominal ridges or diagonal midbody ridges. No lappets, ridges, folds or membranous curtain associated with anal fin. Stomach lightly to darkly pigmented.

Etymology. *Dana*, the Danish research vessel and from the Greek *cetus* (*ketos*) - whale and *ichthys* - fish, in reference to the fine early collection of 33 whalefishes from the *Dana* Expeditions now at the University of

Copenhagen. The gender is masculine.

Remarks. Six specimens have been collected from the Atlantic, Indian and Pacific Oceans. All the specimens are immature and apparently represent one species.

Danacetichthys galathenus n.sp.

Figs 1h, 3d, 4d, 11, 12, 20

Type material. HOLOTYPE: ZMUC P2340563, 39.3 mm, *Dana* 3613 VI, south-west Pacific off New Caledonia, 22°43'S, 166°06'E, 0-ca. 1330 m, 0530 hrs, 28 Nov. 1928.

PARATYPES: 5(34.0-53.9 mm): NSMT P60002 (from TH 821052), 53.9 mm, *Kaiyo Maru* Kocnet 15(B), north-west Pacific off Bonin Is., Japan, 30°25'N, 147°18'E, 0-2046m, 0808-1657 hrs, 10 June 1982; USNM 200525, 53.5 mm, *Anton Bruun* III APB 7014, Indian Ocean, 7°14'N, 59°53'E, 0-2250 m, 3 m IKMT, 1255-1815 hrs, 16 Aug. 1963; ISH 1944/71, 48.6 mm, *Walther Herwig* 459/71, central Atlantic, 10°57'S, 11°20'W, 0-1900 m, CMBT 1600, 1818-2218 hrs, 7 Apr. 1971; SIO 70-327, 38.1 mm, RV *Melville* Ant. 4-630-12, western Pacific, 18°20'N, 133°29'E, 0-1500 m, 1700-0045 hrs, 9 Sept. 1970; ZMUC P2340564, 34.0 mm, *Dana* 1267 II, western Atlantic, 17°56'N, 64°50'W, 0-ca. 1330 m, 0730 hrs, 14 Mar. 1922.

Diagnosis. As for genus.

Description. The holotype is in good condition, with most of the head and lateral line pores as well as papillate neuromasts visible. The NSMT paratype has some skin rubbed off the head and lateral line, but the fins are remarkably complete. Most of the other paratypes are in fair condition, with much skin missing. The ISH specimen has the abdominal wall torn and the stomach protruding. The fins of the SIO specimen are incomplete. The values of the holotype are followed by the range of values of the paratypes in brackets.

D. 14(14-16); A. 15(14-15); P. 21(21-23); principal C. ?(6-8+7); procurrent C. ?(5-6+?); vertebrae 29+16=45 (26-28+15-20=43-46); trunk canal lateral line scales/organs 17(16-18). Measurements in Appendix Table 6.

Body oval in cross section behind head; greatest depth at level of pectoral base. Caudal peduncle 1.3-2.4 times longer than deep. Anus close to anal fin origin. Cavernous tissue extensive around anus only, in series of grooves running dorsoanteriorly from around anus and preanal area; grooves separated by low skin ridges, extending two thirds distance to lateral line tube (Fig. 20a,b). Short, low mid-dorsal ridge, no belly ridge. No anal lappet flaps, scales or ridges at base of anal fin. Subpectoral organ anteroventral to pectoral base visible in best preserved specimens, details of structure unknown.

Head very large, about as deep as wide posteriorly, somewhat depressed anteriorly; head and anterior body profile weakly rounded or slightly concave anteriorly. Nostrils moderate, about half eye diameter, halfway between eye and tip of snout, with raised anterior rim; nasal organ short and low, with no lamellae or ridges, situated almost entirely in anterior nostril (Fig. 1h); internasal skin bridge one third to one quarter nostril diameter. Eye small, with well-developed (2 specimens) or reduced (4 specimens) lens, slightly closer to upper jaw than top of head; strong bony projection of sphenotic over eye.

Mouth enormous, slightly oblique, jaws relatively straight in undamaged specimens; rictus 1-2 eye diameters before posterior end of premaxilla; posterior end of premaxilla closer to edge of gill cover than level of eye; lateral and ventral posterior spines of lower jaw weakly developed. Jaw teeth tiny, very elongate in inner row with basal width more than 3 times in length, those of outer row about one third length of inner; upper jaw with 3(3-4)

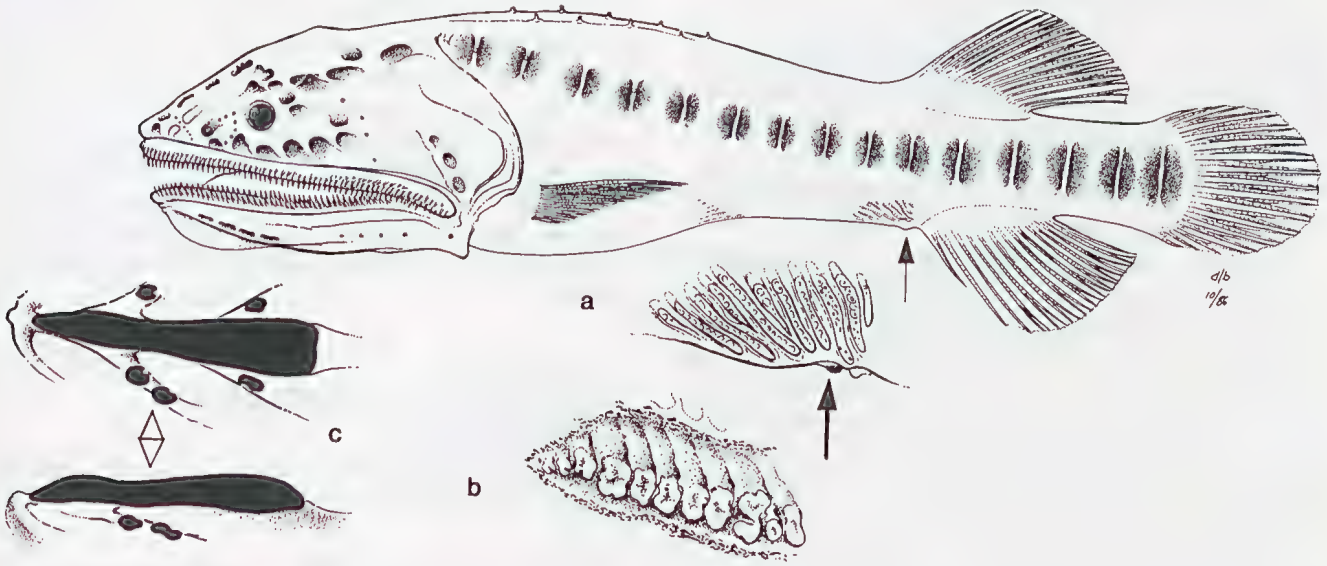

Fig.20. *Danacetichthys galathenus* composite, head and body holotype ZMUC P2340563, 39.3 mm, unpaired fins paratype NSMT P60002, 53.9 mm, arrow indicates level of anus; a, b, enlargement of cavernous tissue; c, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye.

complete rows of teeth and fourth outer row incomplete; 91(93-94 in 2 paratypes) teeth in inner row; lower jaw with 4(3-5) rows of teeth with 71(60-82 in 4 paratypes) in inner row; tooth rows not precise, with some teeth between rows. Vomerine teeth short to moderate, inner teeth longest, in about 3(3-6) rows with 22(15-46) teeth, tooth patch rectangular, ellipsoidal or triangular in shape; palatine teeth moderate to long, inner row longest, in 2-3(2-5) rows with longest row of 16(15-22) teeth; ectopterygoid teeth short to moderate with very small space at end of palatine teeth, in 1(1-2) rows posteriorly and 3(2-4) rows anteriorly with longest row of 38(34-54) teeth, extending about to level of rictus; copular tooth patch short to moderate and wide, pointed anteriorly, rounded posteriorly, broadest posteriorly (Fig. 20c); teeth moderate in length, 7-10(5-13) approximate rows across with about 33(27-40) teeth in length. All teeth depressible towards centre of oral cavity.

Free gill arches 4, with small slit about length of 2 eye diameters behind ventral arm of fourth arch; dorsal arms of arches 1 and 2 free, most of 3 and all of 4 bound together. Holobranchs of all 4 arches well developed and closely spaced, those of first arch about 2.5 times bony width of arch (Fig. 3d); holobranchs of fourth arch about four fifths length of those of first arch; holobranchs absent or present only on ca. 10% of dorsal arm of first arch. Normal gill rakers absent; arch 1 with 2+7(2+7-8) tooth plates, round to elliptical in shape with moderately long, depressible teeth, more than 15 and less than 100 teeth per plate; similar tooth plates on arches 2-4 numbering 1+6(6-8), 1+8(0-1+6-7) and 0+4(3-5), no tooth plates on medial faces of arches. Dorsal pharyngeals as 2 pair of ellipsoid-shaped tooth plates in roof of mouth, posterior about two thirds size of anterior; teeth moderate to long, longest posteriomedially, in indistinct curving rows. Ventral pharyngeal tooth plates of fifth ceratobranchial small and elliptical (triangular to rectangular), covered with small teeth.

Lateral line a broad tube of very thin, fragile overlying skin with 18(17-19) wide pores without flaps or keels, remaining skinbridges much narrower than underlying scales; 17(16-18) underlying scales, round to widely rectangular, flat, without projections, interspaces about half scale width anteriorly, scales almost touching posteriorly; single mid-dorsal row of about 10 papillae from level of top of gill slit to about one third distance to dorsal fin origin, representing dorsal accessory line of neuromasts visible in holotype, presumably rubbed off other specimens.

Lateral line system of head with shallow canals and wide pores, skin mostly torn (Fig. 4d). Supraorbital canal with 6 pores and 5 neuromasts, with fifth and sixth pores large; main canal with 3-4 pores and 3 neuromasts with apparent break between last supraorbital and first main pores; supratemporal pore medial to main pore 2. Infraorbital about 9 pores and 8 neuromasts, last displaced anterodorsally out of series to behind eye, not joined to main canal. Mandibular canal about 8 pores and 7 neuromasts, preopercle about 4 pores, unknown whether joined or not. Group of 5-6 papillate superficial neuromasts on either side of tip of snout, curving row of 10 papillae across internarial bridge of skin, row of 5 papillae between eye and posterior nostril, row of 4-5 widely spaced papillae down preopercle, row of about 20 papillae on posterior half of ventral side of lower jaw.

Dorsal and anal fins far back on body; anal origin under dorsal ray 2-4; ends of dorsal and anal opposite; rays of holotype remarkably complete, middle dorsal and anal rays longest, penultimate 7-8 rays branched at tips. Pectoral fin low, short, directed posteriorly, upper rays longest, no branched rays. Caudal fin weakly rounded (slightly truncate), middle rays longest.

Ovaries of all thin, short, undeveloped, largest paratype with short tubular gonad of orange colour. Paired tubular bladders with transparent walls and connection to dorsal mesentary lateral to ovaries.

Colour in alcohol faded brown; oral cavity light brown; stomach light to dark brown; peritoneum dark brown; intestine without pigment.

Distribution. All six specimens have been taken within 30° of the equator (Fig. 11), in all three oceans.

The species is deeper dwelling than either *Cetostoma* or *Ditropichthys*, as all of the relatively small specimens have been taken with nets fishing to at least 1300 m (Fig. 12).

Etymology. From the Greek *galathenos* - young, in reference to the apparently immature state of all of the type specimens.

Remarks. The six specimens display variation in morphometrics and dentition that is difficult to interpret. The two Atlantic specimens have a much longer caudal peduncle than the other specimens, and have longer dorsal and anal fin bases (Table 6). The three Pacific specimens have more posterior dorsal and anal fin origins than the other specimens. No allometric growth is apparent for any measurement. The most striking differences in dentition are in the number and arrangement of the vomerine teeth. The two smallest specimens have an approximately triangular-shaped tooth patch with the base anterior, about five rows and 19 to 25 total teeth; these specimens come one each from the Pacific and Atlantic Oceans. The other two Pacific specimens, including the largest specimen in the series, have only three rows of vomerine teeth in an approximate rectangle, totalling 15 to 22 teeth. The Indian Ocean and other Atlantic specimen have five to six rows totalling 42 to 46 teeth. Although two or more species may be represented in the series, all are considered one species until more specimens of larger size become available.

Cetostoma Zugmayer, 1914

Cetostoma Zugmayer, 1914: 4. Type species *Cetostoma regani* Zugmayer, 1914 by monotypy.

Diagnosis. *Cetostoma* differs from all other cetomimid genera in having a higher number of dorsal and anal rays (29-37 and 26-34 versus 13-21 and 13-20), elevated dorsal and anal fin bases (versus not elevated) long to very long

(versus moderate to very short), 2.6-4.4 in SL (versus 3.8-14.1 in SL), the dorsal fin origin closer to the snout (distance 1.7-2.0 in SL versus 1.3-1.6 in SL), a very long, narrow copular tooth patch as 3 separate dentigerous plates (versus 1 solid plate), the slit behind the fourth gill arch restricted to a tubular hole behind the angle of the arch (versus a slit behind the ventral arm or none), numerous small skin ridges along the belly from the pectoral base to the anus and the posterior anal fin membrane in curtain-like folds.

Description. D. 29-37; A. 26-34; P. 20-21; principal C. 8-9+7-8=(15)17; vertebrae 23-27+23-26=47-53; trunk canal lateral line scales and organs 15-17. Size large, maximum 246 mm; head moderate to large, 3.2-4.5 in SL and narrow, width at eye 3.8-6.3 in HL; mouth large, jaws extending slightly closer to opercular margin than level of eye; snout rounded and moderate, 2.1-3.1 in HL; dorsal and anal bases long, 0.6-1.3 in HL; caudal peduncle short to moderate, 1.6-2.8 in HL and very slender, 2.8-4.7 in CPL; anus close to anal fin origin, distance 1.5-5.1 in CPD.

Nasal organ short, high and narrow without lamellae or ridges. Eye tiny, 15-41 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores, 6 pores in supraorbital canal, main canal apparently separate from supraorbital canal with 3 pores, infraorbital canal separate from main canal with 9 pores, last not displaced dorsally or anteriorly, mandibular canal with 6-7 pores not joined to preopercular canal with 5 pores; neuromasts large, firm, thin and rectangular. Lower jaw with indistinct lateral spine and distinct ventral spine posteriorly. Jaw teeth tiny, in irregular diagonal bands; vomerine tooth patch variable, oval, rectangular, diamond shaped or asymetrically curved; palatine tooth patch long and slender, extending to level of eye; ectopterygoid tooth patch long and slender, extending behind rictus; copular tooth patch on 3 separate plates, very long and slender with length 1.8-2.0 in HL and width 23-44 in length.

Free gill arches 4, with tube-like slit behind angle of arch 4; holobranchs well developed on first 3 arches, small on fourth arch, present on dorsal arm of first arch. Gill rakers as separate tooth plates on first 3 arches, smaller tooth plates on medial face of arch 1, present or absent on medial faces of arches 2-3; no ventral pharygneal tooth plates.

Lateral line a broad tube pierced by wide pores, with moderate flaps over posterior pores; lateral line scales round, rectangular or diamond shaped, flat. Cavernous tissue in small area immediately before anus. Subpectoral organ visible in smallest, faded specimens. Weak, single midventral ridge along belly. Numerous small, longitudinal ridges of skin between pectoral base and anus. No diagonal midbody ridges. Anal lappets numerous, joined basally, about one per ray for length of fin. Stomach pale, without pigment.

Etymology. From the Greek *cetus* (*ketos*) - whale and *stoma* - mouth. The gender is neuter. There have been unjustified emmendations of the name to *Cetostomus* by some authors.

Remarks. More than 150 specimens have been collected in all three oceans, from 38°N to 40°S in the Atlantic and 43°N to 7°S in the Pacific (Fig. 23). The genus is monotypic.

Cetostoma regani Zugmayer, 1914

Figs 3e, 21-25

"New Genus" Murray & Hjort, 1912: 613, 682, fig. 498 (north Atlantic specimen).

Cetostoma regani Zugmayer, 1914: 3-4. Holotype MOM 3215 from the north-eastern Atlantic, 30°45'N, 25°47'W.

Cetomimus regani.-Parr, 1928: 173-176, fig. 42 (north-eastern Atlantic specimen).-Parr, 1929: 23-27, figs 9,

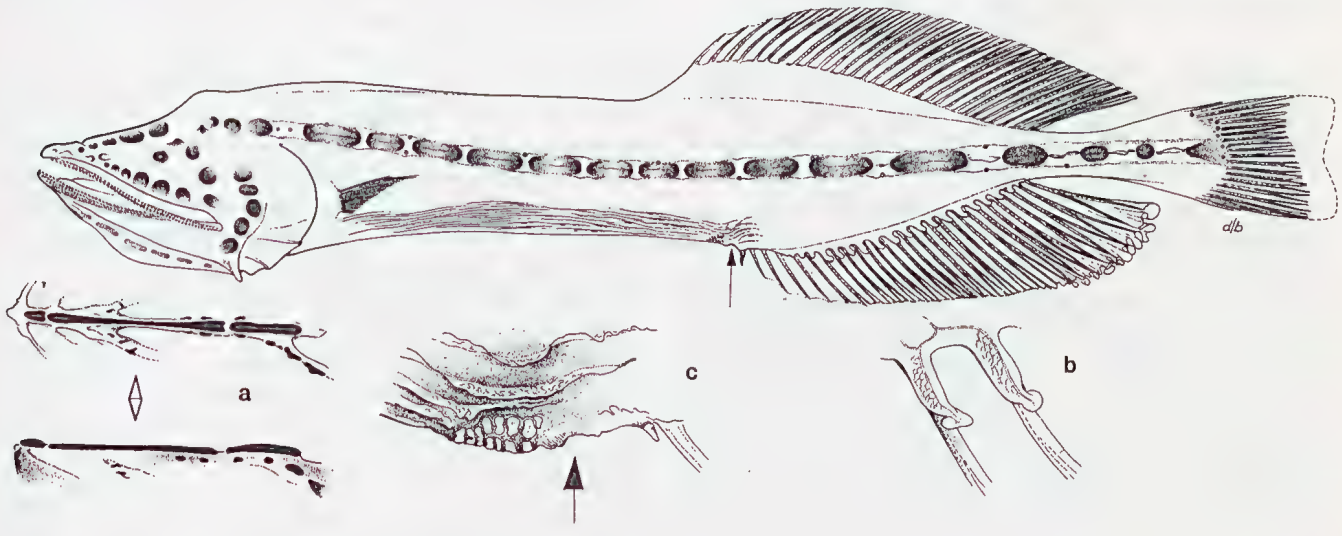

Fig.21. *Cetostoma regani*, 134.0 mm, IOS 10380/5, arrow indicates level of anus; a, copular tooth plates (not to scale), dorsal and lateral views, diamond indicates level of eye; b, anal lappet detail; c, cavernous tissue detail based on ISH 2162/79, 62 mm.

10 (osteology).-Gregory, 1933: 211-212, fig. 92 (osteology repeated from Parr).-Ebeling, 1962: 141 (eastern Pacific specimens listed).-McAllister, 1968: 98 (hyoid arch).

Cetostomus regani.-Parr, 1934: 27-29, fig. 7 (redescription).-Koefoed, 1955: 4-5, pl. II(B) (north Atlantic specimen).-Pearcy, 1964: 87-88 (Oregon specimens listed).-Fitch & Lavenberg, 1968:69 (California specimen).-Kotthaus, 1972: 17, fig. 110 (Indian Ocean specimen, otolith).-Rosen, 1973: 489-492, figs 54, 115 (caudal skeleton, pharyngobranchials).-Herring, 1976: 235-237 (carotenoid pigment).-Fitch, 1979: 63-65, fig. 1e (otolith).

Cetostoma regani.-Harry, 1952:68 (2 Bermuda specimens).-Marshall, 1960: 43 (lack of swimblader) .-Ebeling & Weed, 1973: 397-408, figs 3H, 4F, 5G (osteology, relationships).-Paxton, 1973: 214 (north-eastern Atlantic specimens listed).-Parin *et al.*, 1978: 175 (eastern Atlantic specimens listed).-Maurin *et al.*, 1978: 80 (north-eastern Atlantic specimens listed) .-Hubbs *et al.*, 1979: 10 (California list).-Paxton, 1986: 525, fig. (north-eastern Atlantic specimens).

Cetostomus sp.-Stein, 1985: 190 (north-eastern Pacific specimen listed).

Material examined. See Appendix Table 7. *Cetostoma regani* is apparently the most fragile of all cetomimids; although more than 140 specimens were available, only two specimens had almost all the skin remaining. Complete lateral line pore and scale counts were possible on only five specimens, and only one side of one specimen had the complete number of anal lappet scales over the anal fin. Most specimens had lost all traces of skin and many were broken just behind the head. Dorsal and anal fin rays were counted in all specimens marked * in Table 7; those specimens which were measured are marked **. Vertebrae were counted from x-rays of 40 specimens. The number of tooth patches on the first three gill arches were counted in 17 specimens.

Diagnosis. As for genus.

Description. D. 29-37; A. 26-34; P. 20-21; principal C. (8) 9+(7) 8=(15)17 (8+7 in 1 of 30 specimens counted); vertebrae 47-53; trunk canal lateral line scales/organs 15-17. Measurements in Appendix Table 8.

Body compressed, greatest depth at origin of anal fin. Caudal peduncle 2.8-4.7 times longer than deep. Anus close to anal fin origin. Cavernous tissue immediately around anus, in small adjoining patch in ventral midline anterior to anus. Parallel, thin, transparent ridges of skin running on belly from pectoral base to under first anal fin rays, about 6-10 ridges on each side of ventral midline with dorsalmost ridge about one quarter to one third of way to lateral line (Fig. 21c). No mid-dorsal ridge; weak midventral ridge from level of pectoral base to cavernous tissue. Anal lappets with supporting scales well developed, but easily torn off, beginning under anal ray 4-6 and extending to last 1-3 rays, approximately 1 lappet per ray, but only one complete count of 29 lappets; individual lappets joined at bases but not throughout length; most lappets one third ray length or less (but in 1 LACM specimen 218 mm from the north-east Pacific, lappets more than half ray length), with supporting scales shorter, about half lappet length, ovoid in shape; each lappet with central vessel running length of lappet with many side branches, vessels lateral to lappet scale (Fig. 21c). Subpectoral organ anteroventral to pectoral base visible as darkly pigmented area without apparent pore in 3 faded specimens smaller than 75 mm.

Head moderately large, compressed, deeper than wide posteriorly and somewhat depressed anteriorly; profile from snout to occiput slightly concave, occiput to dorsal origin weakly convex; ventral profile from pectorals to anal weakly concave. Nostrils damaged in almost all specimens, located slightly closer to tip of snout than eye; anterior nostril about half size of posterior with very narrow internasal skin bridge; nasal organ short, high and narrow, without lamellae or ridges, situated mostly in anterior nostril. Eye tiny, with no indication of lens or lens remnant in even smallest specimens, somewhat closer to top of head than upper jaw.

Jaws enormous, angled posteroventrally, upper jaw slightly convex in undamaged specimens; rictus 1-2 eye diameters before posterior end of maxillary; posterior end of jaws somewhat closer to opercular margin than level of eye; posterior lower jaw with indistinct lateral and small, distinct ventral spines. Jaw teeth tiny, triangular, depressible, in indistinct diagonal rows across rounded edges of jaws; dentigerous portions of jaws widest anteriorly, particularly in smallest specimens, posteriormost lower jaw with only 1-2 rows of teeth, extending 1-2 eye diameters behind rictus. Vomerine teeth similar to but smaller than jaw teeth, particularly in large specimens where almost indistinguishable; shape of tooth patch variable, from rectangular to oval to diamond shaped to asymetrically curved as teeth apparently lost with age; palatine teeth intermediate in size between those of vomer and jaws, in approximate diagonal rows in narrow band, beginning at level of vomer in small specimens and anterior to vomer in larger, narrowing posteriorly to end at level of eye; in smallest specimens distance between lateral edge of vomerine patch and palatine teeth about half width of palatine patch, increasing to 1-2 times width of vomerine patch in larger specimens; ectopterygoid tooth band originating slightly before level of eye as 1-2 rows of tiny teeth internal to palatine band and broadening to narrow band behind end of palatine teeth, extending far behind rictus and curving ventrally towards quadrate. Copular tooth patch exceptionally long, more than 10% SL, extending far behind level of eye, in 3 separate patches: first a small oval to rectangular patch usually with tapering posterior extension in larger specimens, a long thin patch extending from just behind first patch to before articulation of second hypobranchials and a third, somewhat rectangular patch shorter than second, extending behind articulation of second hypobranchials (Fig. 21a); 2-5 (usually 3) separate tooth patches on lateral face of second basibranchials ventral to second and third copular tooth patches. Hyoid arch very deep, extending into oral cavity much further than in other cetomimids.

Free gill arches 4, with tiny, tubular slit behind angle of

gill arch 4; about half of dorsal arms of arches 1 and 2 free, dorsal arms of arches 3 and 4 bound together in skin of esophagus. Arch 4 with wide flap of skin around angle and posterior third of ventral arm bearing small, moderately spaced holobranchs; holobranchs of first 3 arches well developed and closely spaced, largest anteriorly on ventral arm decreasing in size towards angle (Fig. 3e); short to moderate holobranchs on one third to two thirds of free dorsal arms of arches 1-2, small holobranchs only around angle of arch 3; anterior holobranchs of arch 1 about 2 times bony width of arch; posterior holobranchs relatively larger in smaller specimens. Normal gill rakers absent; arch 1 with 3-5+8-10 tooth plates rectangular to oval shaped and oriented anteroposteriorly with triangular-shaped ventral extension on lateral face of arch on anterior ventral plates; 0-2+8-11 tooth plates on medial face of arch 1, oval or rectangular shaped and oriented dorsoventrally; arch 2 with 2-3+5-7 lateral and 0-1+3-7 medial tooth plates; arch 3 with 0-1+4-7 lateral and 0+0-3 medial tooth plates; arch 4 edentate; number of tooth plates not correlated to specimen size. Dorsal pharyngeals as 2 pair of oval-shaped tooth plates, first with elongate anterior extension, flatter, less domed than those of other cetomimids; second shorter with straight posterior margin; no ventral pharyngeals; all teeth of gill arches similar to jaw teeth but smaller.

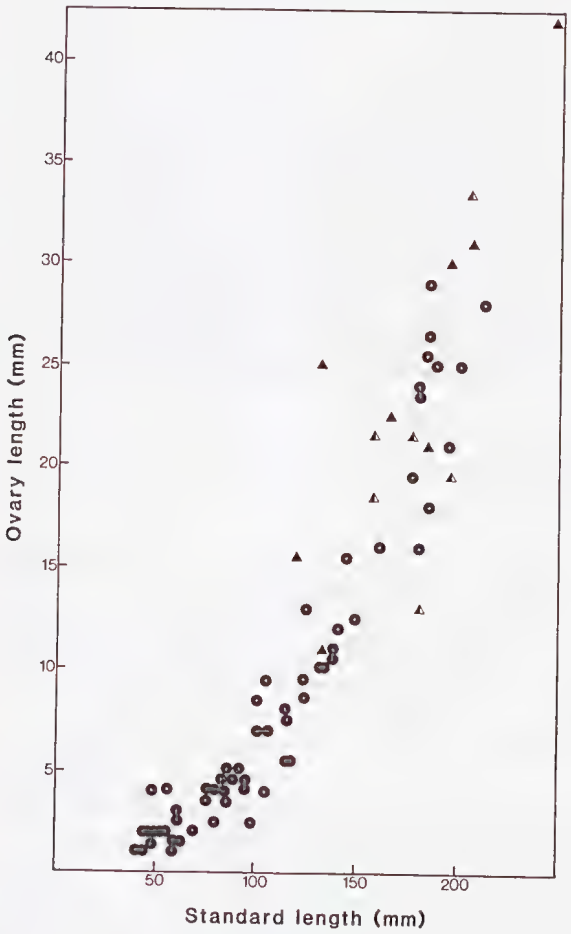

Fig.22. *Cetostoma regani* ovary length versus standard length; triangles indicate egg sizes of 0.1 mm or greater, solid triangles one size class of eggs, half solid triangles with two size classes of eggs.

Lateral line a broad, shallow tube with thin overlying skin, pierced by 16-18 wide pores, anterior pores as wide as canal and rectangular in shape, last 2-3 pores smaller and circular to oval; last 3-4 bridges of skin covering organs and scales between pores with well-developed medial keel of skin, rarely with small posterior flap hanging over pore; skin bridges narrow anteriorly, wide posteriorly; 15-17 lateral line scales oval, rectangular or very rarely diamond shaped, flat, without dorsal or ventral projections, much narrower than interspaces; each scale with very large neuromast overlying central foramen, organ thin, high and rectangular with base oriented anteroposteriorly in lateral line canal. Usually 1-2 dorsal and 1 ventral papillae on undamaged skin bridges and dorsal margins of pores, but not enough complete specimens to determine pattern; 5-6 papillae at base of caudal rays; anterior 2-5 papillae of dorsal accessory line visible on two specimens, widely spaced above gill opening.

Lateral line system of head with shallow, wide canals

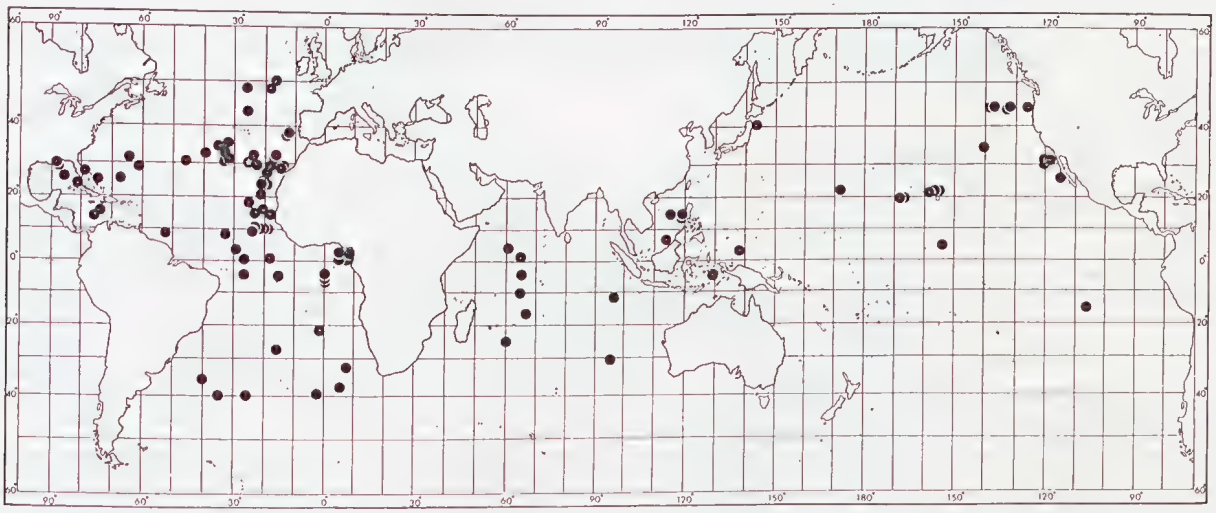

Fig.23. *Cetostoma regani* horizontal distribution; symbols may represent more than one specimen, star indicates holotype.

covered by very thin skin, large pores and very large neuromasts under skin bridges between pores; almost all canal and pore systems torn and damaged in examined specimens, following counts based on two recently caught specimens from the Caribbean: supraorbital canal with 6 pores and 5 neuromasts, fifth pore not close to midline; main canal with 3 pores, first far behind and apparently separate from supraorbital canal, with single supratemporal pore medial to penultimate main pore; infraorbital canal with 9 pores and 8 organs, last far behind eye, not displaced anteriorly or dorsally out of series and not joined to main canal; mandibular canal with 6-7 pores and 5-6 organs, not joined to preopercular canal with 5 pores and 4 organs. Papillate neuromasts very small and unpigmented. Curved row of 5-6 papillae down posterior third of gill cover, vertical row of 4 papillae between posterior tip of premaxilla and fourth preopercular pore, 2 papillae below posterior tip of premaxilla; snouts of all specimens damaged.

Dorsal and anal fins with elevated bases on posterior half of body, very long based; dorsal longer than anal, dorsal origin before and end after those of anal; always more dorsal rays, usually 4 more, range 2-6; first 3-4 rays of each fin heavier and unbranched, all remaining rays branched; unbranched rays shorter, all branched rays subequal in length; membrane between last 10 rays of anal fin thin and extensive with curtain-like folds. Pectoral low, short, directed posterodorsally; all rays except first 2 and last 4-5 branched for about half their length; upper-middle rays longest, last 1-2 rays very short with last ray usually seen only on cleared and stained material. Caudal shape unknown, no fins complete; counts strikingly constant, 9+8 principal rays (8+7 in only 1 of 30 specimens counted).

Ovaries paired, flaccid to rounded in 75 dissected specimens (39.6-246.5 mm), increasing in length with age (Fig. 22). Only 2 specimens with eggs greater than 0.1 mm in

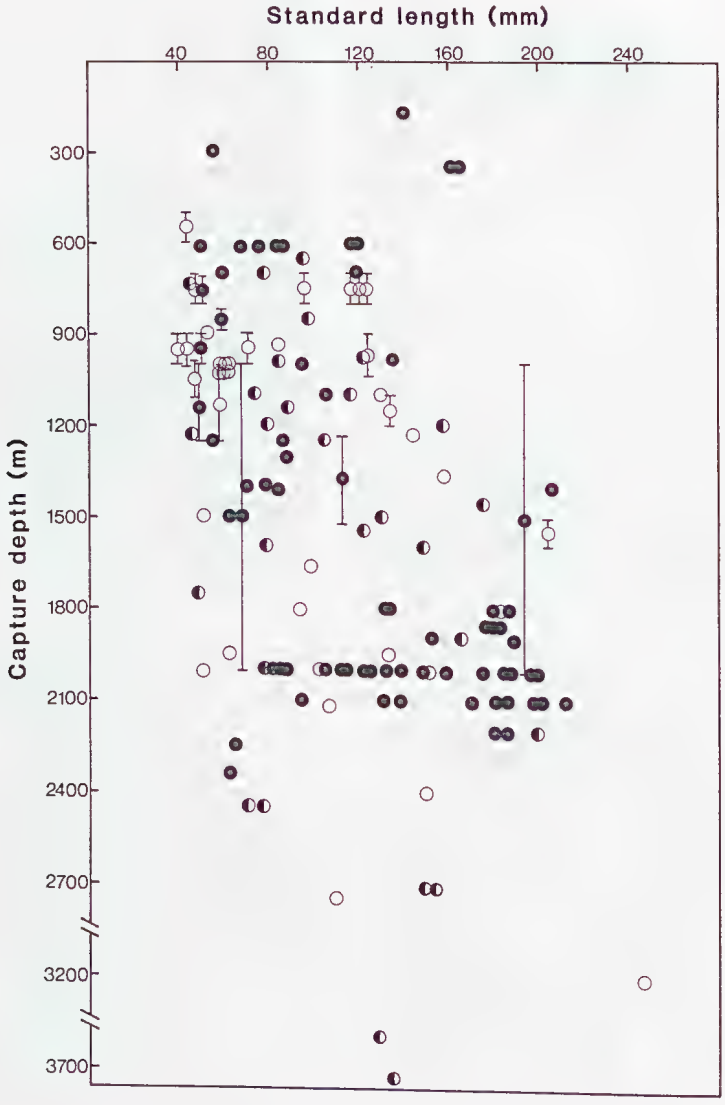

Fig.24. *Cetostoma regani* vertical distribution; open symbols indicate day captures, solid symbols night captures, half solid symbols day/night or unknown time, depths are maximum fishing depths of open nets; closing net captures indicated by vertical bars giving fishing depth limits.

diameter: 131 mm specimen with ovaries 25 mm long by 6 mm wide at anterior end, filled with eggs, all ca. 0.2 mm in diameter and 204 mm specimen with ovaries 33.5 mm by 8.5 mm with few eggs 0.6 mm diameter and most eggs much less than 0.1 mm diameter; of 12 specimens with eggs about 0.1 mm diameter, 7 with all eggs 0.1 mm and 5 with few eggs 0.1 and most much less than 0.1 mm; remaining 61 specimens immature or with eggs less than 0.1 mm. Females apparently do not approach maturity before 125 mm; more than one spawning per lifetime is indicated by the presence of two egg sizes in some ovaries and the range of sizes (120-246 mm) with larger eggs. No males found. Bladder indistinct even is small specimens, apparently single, dorsoposterior to ovaries, oval. Distinct urogenital papilla larger than those of other cetomimids at base of first anal ray.

Colour in alcohol light brown on head, light to dark brown on body and fins; oral and gill cavities, stomach and intestine pale, peritoneum very light brown with scattered melanophores. Colour of two fresh specimens reddish-orange head, black body, dorsal, anal and caudal fins black with bright red edges (W.J. Richards, in literature, July 1988).

Distribution. More than 150 specimens have been collected in all three oceans, from 50°N to 40°S in the Atlantic, 15°N to 31°S in the Indian and 45°N to 15°S in the Pacific (Fig. 23). The lack of captures in the central Atlantic between 10° and 30°N is apparently due to a lack of sampling effort (see Fig. 30), as is the dearth of Pacific captures. *Cetostoma regani* has the broadest distribution of any cetomimid.

The 17 diurnal captures with closing nets (by IOS) give the best picture of vertical distribution of any cetomimid (Fig. 24). A normal diurnal distribution between 700 and 1200 metres is indicated. The shallowest diurnal capture (500-600 m) is of one of the smallest specimens (43 mm) and the deepest (1500-1600 m) is of one of the largest (204 mm), indicating a trend for the diurnal depth to increase with increasing size, similar to the picture for *Ditropichthys storeri*. Nocturnally a limited vertical migration to 600 to 700 m is indicated by eight open net captures of specimens less than 125 mm; migration to 110 to 400 m occurs rarely, with only five of 150 specimens taken above 600 m.

Etymology. After C. Tate Regan of BMNH.

Type specimen. The holotype, MOM 3215, is a small specimen in poor condition, with few remnants of skin and no lateral line pores or anal lappets remaining. The fin rays and jaws are broken and the body badly distorted; accurate measurements were impossible for most features. Nevertheless the high number of dorsal and anal fin rays, elongate fin bases and three separate copular tooth plates result in an unquestionable identification.

Remarks. Two specimens with dorsal ray counts of 35 and 37 were labeled as ms holotypes of new species (ZMUC P2340565 and USNM 200530). Dorsal and anal fin ray counts were made on a total of 103 specimens (Fig. 25) and only nine specimens had dorsal ray counts over 34; four of these were collected in the north Atlantic, two in the Indian Ocean and one in the west Pacific. No other feature of morphology, dentition or morphometrics distinguished these nine specimens from other measured specimens with 29 to 34 dorsal rays, although many of the specimens were badly damaged and features of the lateral line system on the head and body could not be detailed for most. The nine specimens represent the tail of a normal bell-shaped curve for the distribution of dorsal rays (Fig. 25) and are considered part of the normal variation of *C. regani*.

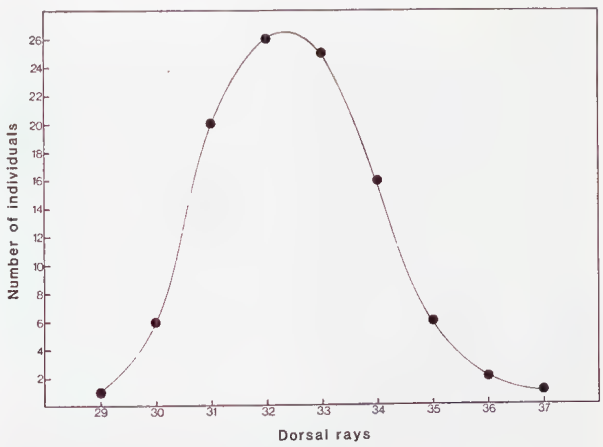

Fig.25. *Cetostoma regani* distribution of dorsal finray numbers in 103 specimens.

Measurements were made on 22 specimens from 48 to 246 mm (Table 6). Analyses of the measurements of three size classes (48-79, n = 5; 96-125, n = 7; 183-246, n = 11) indicate that the relative lengths of the head, jaws and snout to pectoral, dorsal and anal distances are longest in the smallest size class, but not different in the two largest classes, while relative body depth and eye width are greatest in the largest specimens (Table 8). Allometric growth over all three size classes is apparent for eye diameter, dorsal origin to anal origin and caudal peduncle length. The four measured specimens from the Indian and Pacific Oceans did not show significant differences from the 18 Atlantic specimens and only one species of *Cetostoma* is currently apparent.

Gyrinomimus Parr, 1934

Figs 1j, 2c, 3g, 4e, 5c, 7b, 8a, 26

Gyrinomimus Parr, 1934: 29. Type species *Gyrinomimus myersi* Parr, 1934 by monotypy.

Diagnosis. *Gyrinomimus* has elongate, closely-set teeth in distinct rows in the jaws and palate, unlike all other cetomimid genera except *Danacetichthys*. *Gyrinomimus* differs from *Danacetichthys* in the number of free gill arches (3 versus 4), form of gill "rakers" (solid, flat tooth plates covering most of lateral face of arch versus separate, round, domed tooth plates), absence of ventral pharyngeal

tooth plates (versus present), vertebral number (47-59 versus 43-46), lateral line scale shape (narrowly rectangular or strap like and curved versus round or widely rectangular and flat) and maximum size attained (390 mm versus 54 mm). *Gyrinomimus* is most similar to *Cetomimus*, differing only in the teeth (elongate in distinct longitudinal rows in all but two species versus short in distinct or indistinct diagonal rows) and the shape of the vomerine tooth patch (rectangular or laterally elongate and flat versus round or elliptical and dome shaped).

Description. D. 14-21; A. 14-20; P. 18-23; principal C. 13-16; vertebrae 26-39+16-24=47-59 (n=105); trunk canal lateral line organs and scales 12-23. Range of measurements based on 60 specimens of at least 8 species in Appendix Table 9. Size very large, maximum attained 390 mm; head moderate to very large, 2.7-3.9 in SL and wide, width at eye 2.0-2.9 in HL; mouth large to very large, jaws ending much closer to opercular margin than to level of eye; snout rounded and moderate in length, 2.7-3.9 in HL; dorsal and anal bases short to moderate, 1.3-2.6 in HL; caudal peduncle short to long, 2.0-4.2 in HL and slender to moderate, 1.1-3.3 in CPL; anus close to anal fin origin, distance 2.0-9.3 in CPD.

Nasal organ small to moderate, mostly in anterior nostril, usually with low lamellae in larger specimens. Eye tiny, 17-61 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores; supraorbital canal with 6-7 pores, separate from main canal of 4-5 pores; infraorbital canal separate from main canal with 8-10 pores, the last displaced anterodorsally out of series; mandibular canal with 6-11 pores, joined to preopercular canal with 1-5 pores; neuromasts moderate in size. Lower jaw with well-developed lateral and ventral spines or projections posteriorly. Jaw teeth long, width at least 3 in length, closely set, usually in distinct longitudinal rows, rarely with both diagonal and longitudinal rows; vomerine tooth patch rectangular or laterally elongate and flat; palatine and ectopterygoid tooth patches slightly separated, latter long and extending to or beyond level of rictus; copular tooth patch in 1 plate, short to long, 2.6-4.9 in HL, and narrow to broad, 1.8-7.6 in length, shield shaped.

Free gill arches 3, no slit behind ventral arm of fourth arch; holobranchs well developed on first 3 arches, tiny to large on fourth arch. Gill rakers as tooth plates on all 4 arches; tooth plates present or absent on medial face of arches; no ventral pharyngeal tooth plates.

Lateral line a broad tube pierced by wide to tiny pores, flaps and keels present or absent; lateral line scales strap shaped or narrowly rectangular, curved, often with terminal projections of 1-3 spines. Cavernous tissue in small area or extensive around anus and often at other areas (along dorsal and anal rays, predorsally, dorsolaterally above pectoral, posterior lateral line). Subpectoral organ present or absent. No paired abdominal ridges or diagonal midbody ridges. Anal lappets present or absent, if present from 3-14 separate lappets over anal base; no other flaps, ridges or membranous curtain associated with anal fin. Stomach darkly pigmented.

Etymology. From the Greek *gyrino* - tadpole and *mimus* - like. The gender is masculine.

Remarks. More than 125 specimens have been collected from all three oceans. *Gyrinomimus* is the most widespread of all cetomimid genera, extending from 52°N in both the Atlantic and Pacific to 59°S in the Atlantic and 72°S in the Pacific.

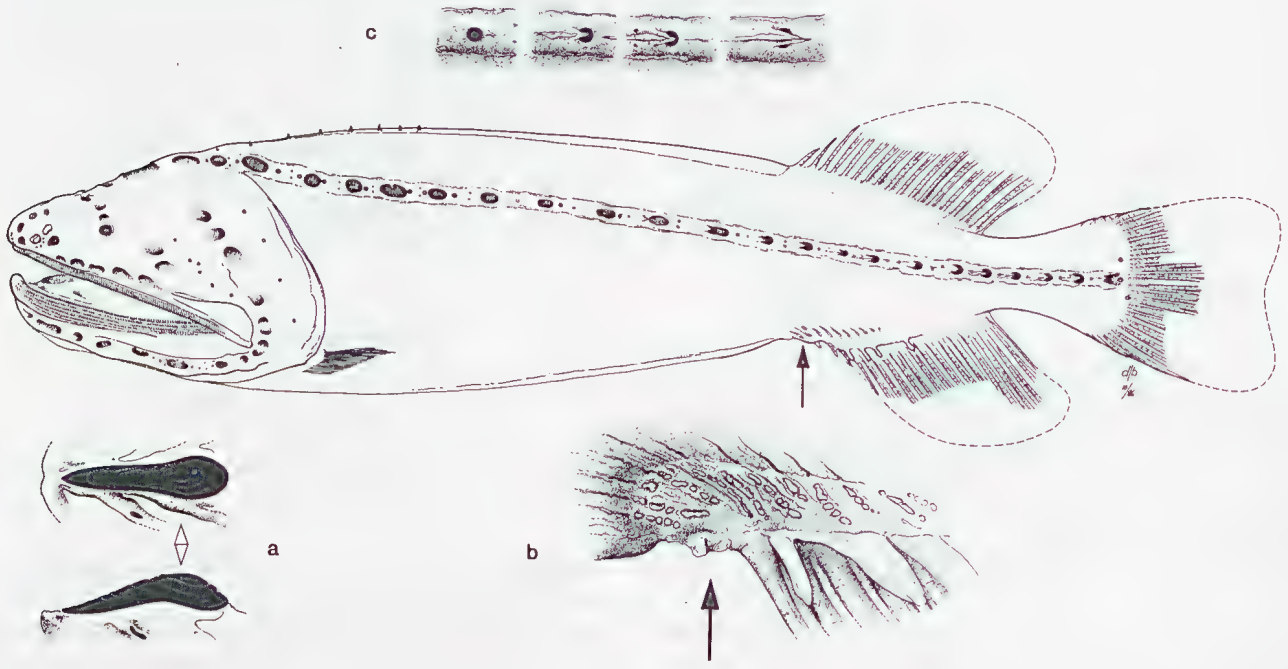

Fig.26. *Gyrinomimus* sp. C, 272.0 mm, LACM 6903-21, arrows indicate level of anus; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, detail of cavernous tissue and first anal lappets; c, detail of lateral line pores.

Gyrinomimus contains seven nominal species (Table 1) and is currently being revised. The recognition of *G. notius* and *G. parri* as junior synonyms is based on the fact that tooth rows are added to the jaws and palate with growth and the number of vomerine tooth rows was considered diagnostic in both original descriptions. Variation in other characters is still being studied, but at least four new species await description. Specific characters include presence and number of anal lappets, size of fourth holobranch, distribution of cavernous tissue, number and shape of lateral line pores, shape and number of spines on lateral line scales, number and distribution of tooth plates on the gill arches and number of vertebrae and dorsal and anal rays.

Cetomimus Goode & Bean, 1895

Figs 1k, 2f, 3h, 4f, 7a, 27

Cetomimus Goode & Bean, 1895: 452. Type species *Cetomimus gilli* Goode & Bean, 1895 by subsequent designation of Jordan & Evermann, 1896: 549.
Pelecinomimus Gilchrist, 1922: 56. Type species *Pelecinomimus picklei* Gilchrist, 1922 by monotypy.
Cetomimus (*Psapharocetus*) Harry, 1952: 59. As subgenus, type species *Cetomimus kerdops* Parr, 1934 by original designation.

Diagnosis. *Cetomimus* has no single, derived character to distinguish it from all other genera. Like *Rhamphocetichthys* and *Gyrinomimus*, *Cetomimus* has only three free gill arches. *Cetomimus* differs from *Rhamphocetichthys* in lacking ventral pharyngeal tooth plates, in having a cavernous lateral line system of large canals pierced by wide pores on the head and body and in having a much shorter, rounded snout. *Cetomimus* is most similar to *Gyrinomimus*, differing in the form of the teeth (short in indistinct, diagonal rows versus long in distinct, usually longitudinal rows) and in the shape of the vomerine tooth patch (round or elliptical and dome shaped versus rectangular or laterally elongate and flat).

Description. D. 15-20; A. 13-20; P. 17-23; principal C. 14-16; vertebrae 24-34+15-20=44-54 (n=30); trunk canal lateral line scales and organs 10-24. Range of measurements, based on 15 specimens of at least 6 species in Appendix Table 9. Size large, maximum 256 mm; head moderate to very large, 2.3-3.4 in SL and wide, width at eye 1.9-2.9 in HL; mouth large to very large, jaws ending much closer to opercular margin than level of eye; snout rounded and moderate, 2.5-2.9 in HL; dorsal and anal bases short to moderate, 1.4-2.8 in HL; caudal peduncle very short to moderate, 2.2-4.1 in HL and slender to deep, 1.3-3.6 in CPL; anus close to anal fin origin, distance 3.1-5.5 in CPD.

Nasal organ small to moderate, mostly in anterior nostril, many species with ridges or reduced lamellae on rounded nasal organ. Eye tiny, 13-39 in HL, without discernible lens. Lateral line system of head a series of large canals with wide pores; supraorbital canal with 6-7 pores, separate from main canal with 4-5 pores; infraorbital canal separate from main canal with 8-9 pores, last displaced anterodorsally; mandibular canal with 6-9 pores, joined to preopercular canal with 3-4 pores; neuromasts moderate in size. Lower jaw with well-developed lateral and ventral spines or projections posteriorly. Jaw teeth short, width less than 2 in length, closely set in indistinct rows; vomerine tooth patch round or elliptical and dome shaped; palatine and ectopterygoid teeth slightly separated, latter extending to or beyond level of rictus; copular tooth patch on 1 plate, moderately long, 3.0-6.3 in HL and broad, 3.3-5.8 in length.

Free gill arches 3, no slit behind ventral arm of fourth arch; holobranchs well developed on first 3 arches, tiny to large on fourth arch. Gill rakers as tooth plates on all 4 arches; usually no tooth plates on medial face of arches; no ventral pharyngeal tooth plates.

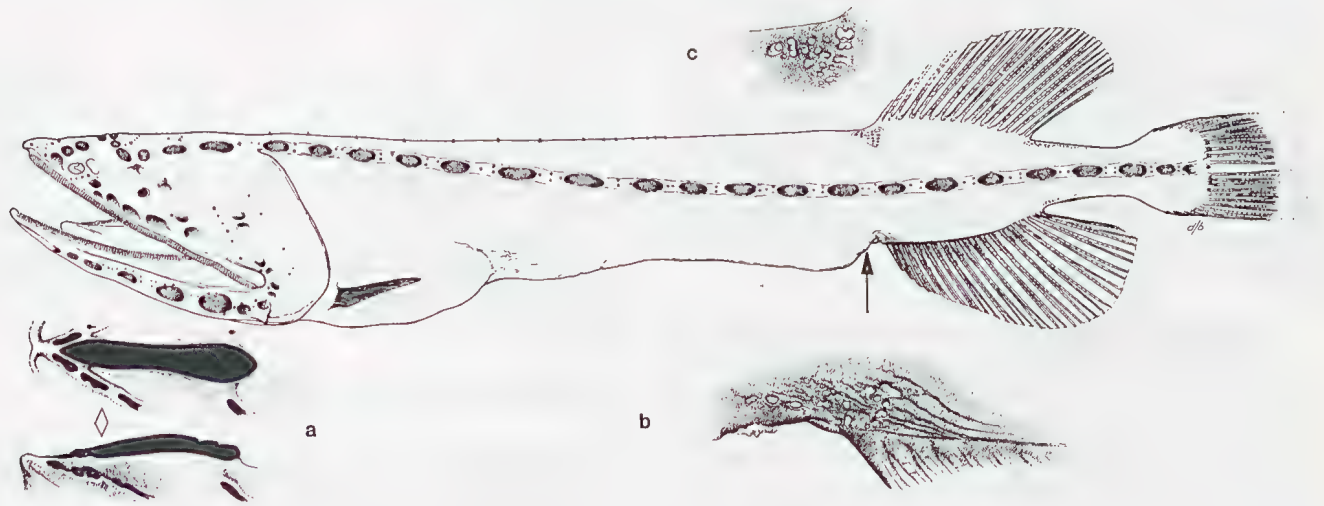

Fig.27. *Cetomimus* cf. *compunctus*, 124.7 mm, ZMUC *Dana* 1208 IV, arrow indicates level of anus; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, detail of cavernous tissue before anal fin; c, detail of cavernous tissue before dorsal fin.

Lateral line a broad tube pierced by small to wide pores with flaps and keels present or absent; lateral line scales strap shaped or narrowly rectangular, curved, often terminating in 1 spine. Cavernous tissue in small area or extensive around anus, and often at other areas (along anal and dorsal rays, predorsally, caudal peduncle, isthmus, posterior lateral line, flap on posterior upper jaw). Subpectoral organ present in some species. No paired abdominal ridges or diagonal midbody ridges. No anal lappets with internal scales; skin fold present or absent along anal base; skin ridges associated with anterior anal rays often present; no membranous curtain joining posterior anal rays. Stomach darkly pigmented.

Etymology. From the Greek *cetus* (*keto*) -- whale and *mimus* -- like. The gender is masculine.

Remarks. More than 180 specimens have been collected from all three oceans, extending from 41°N in the Pacific and Atlantic to 40°S in the Atlantic and 57°S in the Pacific.

Cetomimus contains seven nominal species (Table 1) and a revision of the species has just begun. *C. gilli* and *C. picklei* are in the same species group, as are *C. craneae* and *C. compunctus*. Study of variation is required, but at least five new species await description. Recognition of subgenera requires re-evaluation of all species groups. Specific characters include the number and shape of lateral line pores and flaps, distribution of cavernous tissue, size of the fourth holobranch and number of dorsal and anal rays and vertebrae.

Rhamphocetichthys n.gen.

Type species. *Rhamphocetichthys savagei* n.sp.

Diagnosis. *Rhamphocetichthys* differs from all other cetomimid genera in the development of an elongate, pointed snout 5.1-6.2 in SL (versus rounded and 6.5-14.1 in SL) with the upper jaw overhanging the lower, in the lack of a cavernous lateral line system on the head and tooth plates on gill arches 2-4, and in the high number of lateral line scales (31-40 versus 8-24). Unlike all other members of the subfamily Cetomiminae, *Rhamphocetichthys* lacks a lateral line canal pierced by pores on the body and cavernous luminous tissue around the anus, characters shared only with *Procetichthys*.

Description. D. 15-17; A. 15-17; P. 21-24; principal C. 16; vertebrae 27-29+16-17=43-45; trunk lateral line organs and scales 31-40. Size moderate, maximum known 126 mm; head very long, 2.6-2.9 in SL, and narrow, width at eye 6.6-10.1 in HL; mouth very large, jaws ending much closer to opercular margin than to level of eye; snout very elongate and pointed, 1.9-2.2 in HL; dorsal and anal bases short, 2.7-3.8 in HL; caudal peduncle moderate to short, 2.3-3.0 in HL, and very slender, 2.5-4.5 in CPL; anus close to anal fin origin, distance 1.0-4.3 in CPD.

Nasal organ small and high, without lamellae or ridges. Eye tiny, 21-26 in HL, without discernible lens. Lateral line system of head a series of small, widely-spaced superficial neuromasts. Lower jaw with blunt lateral and ventral projections posteriorly. Jaw teeth tiny, triangular in diagonal rows; vomerine teeth at least 5; palatine and ectopterygoid teeth separate, latter extending beyond rictus with enlarged posterior teeth; copular tooth patch on 1 plate, moderate with length 3.6-4.2 in HL and moderate to broad, width 4.6-7.3 in length.

Free gill arches 3, no slit behind fourth arch; holobranchs well developed on all 4 arches, absent on dorsal arm of first arch. Gill rakers as separate plates (4-11 on first arch) of tiny teeth, none on medial face and no tooth plates on arches 2-4; ventral pharyngeal tooth plates on fifth ceratobranchial present.

Lateral line a series of vertical rows of papillate superficial neuromasts, 1-3 per row; no lateral line canal or pores; lateral line scales rectangular and flat. No cavernous luminous tissue. Subpectoral organ present. No paired abdominal ridges or diagonal midbody ridges. Anal lappets separate, 4-9; no ridges, folds or membranous curtain associated with anal fin. Stomach with very light brown pigment.

Etymology. From the Greek *rhamphos* - curved beak, *cetus* (*ketos*) - whale and *ichthys* - fish, in reference to the beak-like snout. The gender is masculine.

Remarks. Only four specimens, which presumably represent one species, have been collected from bathypelagic waters of the Pacific and Atlantic Oceans.

Rhamphocetichthys savagei n.sp.

Figs 1i, 2d, 3f, 4g, 11, 12, 28

Type material. HOLOTYPE: MCZ 60342, 125.7 mm, GRH 1042, Coral Sea, 12°22'S, 146°29'E, 0-ca. 1000 m, 30 Nov. 1981.

PARATYPES: LACM 30034-11, 90.8 mm, *Velero IV* 11733, Gulf of California, Mexico, 20°51'N, 106°28'W, 0-1400 m, 0700-1515 hrs, 8 Nov. 1967; AMS I.26872-001 (exLACM 30042-11), 98.5 mm, *Velero IV* 11764, Gulf of California, Mexico, 23°24'N, 108°17'W, 0-1400 m, 1015-1845 hrs, 15 Nov. 1967.

Other material. ISH 2297/71, 110 mm, *Walther Herwig* 478/71, central Atlantic, 01°04'N, 18°22'W, 0-2100 m, 12 Apr. 1971.

Diagnosis. As for the genus.

Description. The holotype is in good condition except the upper and lower jaws have parted at the ricti and the specimen has been preserved with the mouth wide open and jaws distorted. Both paratypes have faded and torn skin and ruptured abdominal cavity; the larger paratype has lost the anterior tip of one upper jaw. The fourth

specimen is in poor condition, with the tips of the upper jaws broken, the ventral body wall torn, the body distorted and skin missing anterior to and under the dorsal fin. Values of the holotype are followed by those, if different, of the paratypes in brackets with those of the fourth specimen following a semicolon.

D. 17(15;15?); A. 17(15); P. 23/24(21-23;22); principal C. 8+8, procurrent C. ?(6+6; ca. 5+5); vertebrae 27+16=43(27-28+16-17=44;29+16=45); lateral line scales and organs 33(31-32;40). Measurements are given in Appendix Table 6.

Body oval in cross section behind head. Greatest depth at pectoral fins. Caudal peduncle 2.5-4.5 times longer than deep. Anus before anal fin by distance equal to one quarter (half to two thirds) caudal peduncle depth. Striated tissue, possibly homologous to cavernous tissue, on lateral line between scales and at caudal base (Fig. 28b). No cavernous tissue around anus. Low mid-dorsal ridge present; small midventral fold from anus anterior to one third of way to head present in one paratype. Anal lappet scales 8-9 (1-3 scars; 5-6 scars) over anterior anal fin bases (Fig. 28c). Subpectoral organ distinct in holotype as dark body beneath skin, anteroventral to pectoral base with possible pore in skin, unclear in faded paratypes.

Head large and very compressed, head width approximately half head depth. Snout greatly elongated, eye about midway between tip of snout and edge of operculum. Head profile smoothly rounded except for bony projection behind eye. Nostrils large, without raised rims, nearer to eye than tip of snout and close to upper jaw; posterior nostril about 50% larger than anterior; internasal bridge of skin about half diameter of anterior nostril; raphe moderate (short), high and narrow or rounded, without lamellae or ridges (Fig. 1i). Eye small, without lens or much apparent structure, midway between upper jaw and profile of snout. Interorbital narrow, convex with bony projection just behind eye.

Mouth enormous; premaxilla evenly concave, extending anteriorly beyond lower jaw; dentary concave posteriorly, anterior tip downturned to fit behind and between anterior tips of premaxillae; approximately one fifth (half) of anterior downturned border of dentary edentate; anteriormost lower jaw with a median soft projection; rictus approximately one eye diameter before posterior tip of premaxilla; jaws extend almost to gill cover; mandible with small blunt lateral projection posteriorly, tip of angular produced into blunt spine ventrally. Jaw teeth granular, in many irregular series on both jaws (Fig. 2d,e); individual teeth tiny with flattened, trapezoidal-shaped base set in jaw socket; upright tooth shorter than base length, arising from lateral edge of base, triangular and laterally compressed; all jaw teeth point towards centre of oral cavity; dentigerous edge of jaws slightly rounded; teeth in approximately diagonal series, with about 75 (65-85;48) series of 3-6(2-5) teeth each in premaxillary and 37(60-64;38) series of 6-9(5-6) teeth on the dentary, extending posteriorly slightly behind rictus. Individual teeth of palate and hypobranchial arches similar to jaw teeth, but most much smaller; vomerine teeth lost, sockets not countable(at least 5 in one paratype), slightly closer to tip of premaxillary than eye; palatine teeth in 1(1-3;1-2) rows, with 6/7(13-15;15) teeth in longest row; edentate space between palatine and ectopterygoid half to two thirds eye diameter; ectopterygoid teeth in 1-1.5 (2-5;1-2) series, 31/32(43;34) in longitudinal row, increasing in size posteriorly, with posterior 3-4 teeth as tiny canines; edentate space (absent; absent) before these 4 posteriormost teeth. Copular tooth patch elongate, 2.1 (1.7-1.9;2.3) in snout, modified dumb-bell shaped with posterior end widest and emarginate (Fig. 28a); 31 (32-36;27) teeth in longitudinal series.

Free gill arches 3, no slit behind fourth; most of dorsal arms of gill arches bound together. Holobranchs long but widely spaced, those on ventral edge of first arch about twice as long as bony width of arch (Fig. 3f); holobranchs of fourth arch as long as those on first arch; no holobranchs on dorsal arm of first arch. Normal gill rakers absent; first arch with 1(3;0-1) epibranchial, 6(6-7;4-5) ceratobranchial and

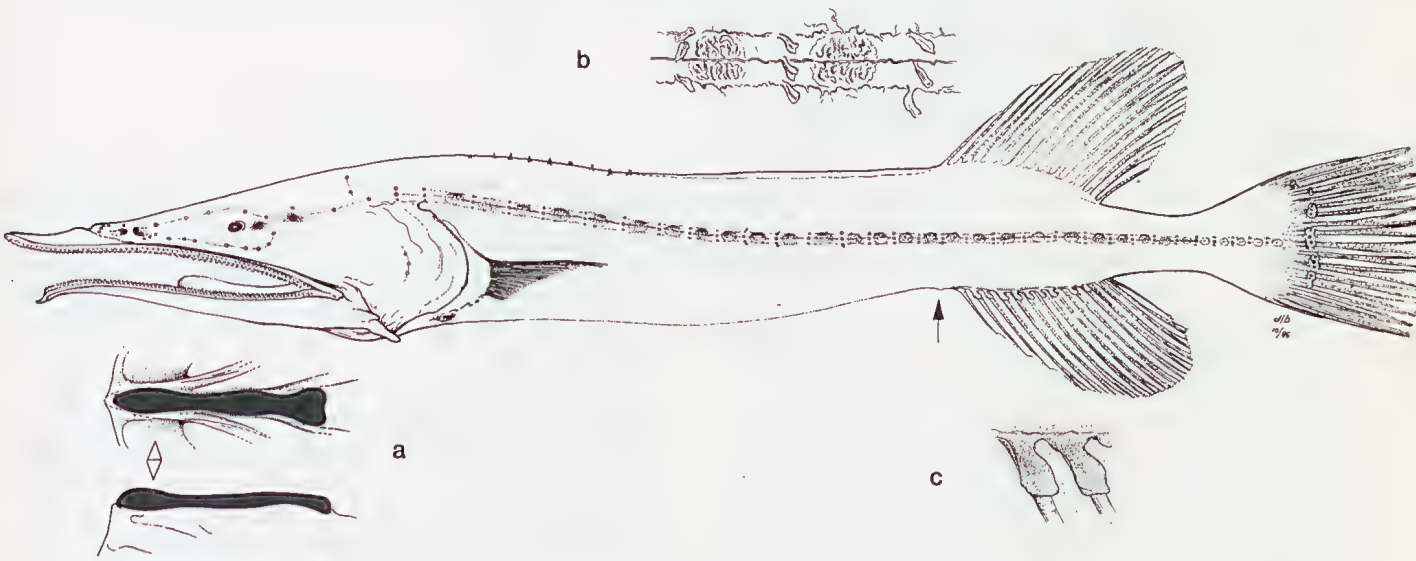

Fig.28. *Rhamphocetichthys savagei* holotype, 125.7 mm, MCZ 60342, arrow indicates level of anus; a, copular tooth plate (not to scale), dorsal and lateral views, diamond indicates level of eye; b, detail of lateral line; c, detail of anal lappets.

1-2(0-1;0) hypobranchial lateral tooth plates; 1-7(;1-3) teeth per plate with largest the posteriormost plate of ceratobranchial; no tooth plates on medial face of arch, or on epi-, cerato- or hypobranchials of arches 2-4. Dorsal pharyngeals as 2 pharyngobranchial tooth plates on each side of roof of mouth; anterior (third pharyngobranchial) toothplate elongate and slightly curved, pointed (rounded) anteriorly and rounded posteriorly; 3-6(3-8;2-5) irregular rows of teeth with 12(13-22;12) teeth in longest row; posterior plate short, about 2.5 in length of anterior plate, with 2-4(1-5;2-3) irregular rows of teeth and 6-7(7-11;5) teeth in longest row; paired ventral pharyngeals of fifth ceratobranchials as curved plates with pointed ends, almost twice as long as posterior dorsal plates, with some 2-6 long rows of teeth and 11(14-18;11) teeth in longest row. The dorsal and ventral elements of the hypobranchial tooth plates do not contact as the dorsal pharyngeals are over the space between the copula and ventral pharyngeals.

Lateral line not a broad tube, but a shallow, wide trough with weak folds of skin along dorsal and ventral margins of trough; 33(31-32; ca. 40) scales from top of gill cover to caudal base embedded under skin of bottom of trough; each scale rectangular with central pore through which runs branch of lateral line nerve; skin overlying scale with central neuromast, the main lateral line organ, and single more slender elongate papillae above and below. Free fold of skin originating in dorsal midline behind head and increasing in size to dorsal fin origin; dorsal accessory line of superficial neuromasts as 2 parallel rows of papillae on anterior half of fold, about 9 papillae per row, paired anteriorly and alternating posteriorly. In paratypes, skin faded so small paired nerves visible running length of fold with branch to each neuromast.

No cavernous lateral line system present on head. Superficial neuromasts similar to those in lateral line represent neuromasts found in head canals of other cetomimids, with similar arrangement (Fig. 4g); in some areas a nerve connects a line of neuromasts. Only holotype with discernible head system, paratypes too faded and skin of head of fourth specimen badly torn. Supraorbital line from tip of snout to behind eye with 5 neuromasts, joined to main line with 5-6 neuromasts and supratemporal line with 3 papillae. Two typical lateral line organs with 3 papillae each, presumably with underlying scales, between main line and top of gill slit. Infraorbital line under eye from posterior nostril with 8 neuromasts; line across ventral preopercle with 4 neuromasts, mandibular line with 5-6 neuromasts, line ventrolateral to nostrils with 9 papillae and 2 series across anterior head, one anterior to nostrils with 3 papillae on each side and one at level of anterior nostril with 1 papilla; connections between each branch not clear, total number of neuromasts in all series approximate.

Dorsal and anal fins far back on body; anal origin under third dorsal ray; ends of dorsal and anal bases opposite; tips of most rays broken but posterior rays obviously much longer than anterior rays, longest rays branched at tips in holotype. Pectoral fin low, short, directed obliquely upward with few longest rays branched only at tips; ventralmost 6 rays much shorter than upper rays. Caudal ray ends broken.

Gonads of holotype about 10 mm long, flattened, whitish; gonads of 1 paratype thin and undeveloped, other 2 specimens torn, sex of all specimens indeterminate. Bladder paired, very short and wide, almost round.

Colour in alcohol medium brown (faded in paratypes). Oral cavity light brown, stomach with some light brown pigment, intestine without pigment except posterior one fifth weakly orange in holotype; peritoneum dark brown.

Distribution. With records from the Coral Sea, Gulf of California and central Atlantic (Fig. 11), the species (if only one) is broadly distributed within 25° of the equator.

All four captures were made with open nets fishing to between 1000 and 2100 m (Fig. 12).

Etymology. After Jay M. Savage, who gave the author opportunity and encouragement as a student and developed the midwater trawling programme which collected the two LACM paratypes, in recognition of his contributions in biology.

Remarks. Before the fourth specimen, the holotype, became available the three smaller specimens were considered to represent two species, distinguished by differences in lateral line organ and scale numbers, size and numbers of teeth in the jaws (Fig. 2d,e) and ectopterygoid and size of the edentate area at the tip of the lower jaw. The holotype has the lower number of lateral line organs similar to the Mexican specimens and some lower tooth numbers similar to the Atlantic specimen. At least in some species of *Gyrinomimus*, tooth numbers increase rather than decrease with growth. While it is possible that three species are represented by the four specimens, only one is named until more specimens in undamaged condition are collected.

Other cetomimids collected in the same haul as the ISH specimen include *Cetomimus* sp., *C. compunctus*, *Cetostoma regani* and *Ditropichthys storeri*.

Relationships

The establishment of derived character states for use in a phylogenetic analysis of relationships can be based on outgroup comparisons of related taxa (fossil or Recent) and ontogenetic transformations. For cetomimids, neither fossils nor larvae nor juveniles less than 25 mm are known, and outgroup comparison is the method used to polarise character states.

Family relationships of the Cetomimidae have not been adequately established. Within the last 20 years at least 20 families, mostly in the orders Stephanoberyciformes and Beryciformes, have been hypothesised as relatives of the Cetomimidae (Greenwood *et al.*, 1966; Myers & Friehoffer, 1966; Rosen & Patterson, 1969; Ebeling & Weed, 1973; Rosen, 1973). A full outgroup analysis would include the character states for representatives of these 20 families, but is beyond the scope of the present paper. Virtually every

author has considered the Rondeletiidae and Barbourisiidae as the closest relatives of the Cetomimidae, with Rosen (1973) and Ebeling & Weed (1973) justifying their classifications with osteological characters. The outgroup analysis has been restricted to the monotypic *Barbourisia* and the two species of *Rondeletia*; both are the only genera of their respective families.

Genera rather than species of cetomimids are used in the distribution of character states (Appendix Table 10) and the computer analyses that follow. The genera are clearly distinguishable (see the Key to Genera above). While the species composition and relationships within each genus are valid subjects for analysis in their own right, the species revisions of *Gyrinomimus* and *Cetomimus* required for such analyses have not been completed.

Specimens of *Rondeletia* and *Barbourisia* used for morphometrics and other character distributions are listed in Materials and Methods. More complete ranges of meristics were taken from Paxton (1974) for *Rondeletia* and from unpublished data for *Barbourisia*. In the following discussion, characters are described in the order they are given in the generic descriptions and numbered for reference (Table 10; Fig. 29). In all cases but one, characters are restricted to those that could be polarised unequivocally using both outgroup families. The relationships of the two outgroup families to each other are unresolved (Fig. 29). Therefore when a character showed two states, one in each of the two outgroups, it was not used.

Four features, pelvic fins, pleural ribs, gill rakers/tooth plates on the medial side of the fourth gill arch and pyloric caeca, are present in *Rondeletia* and *Barbourisia* and absent in all cetomimids examined. To determine whether these three characters of loss are synapomorphic for the Cetomimidae (at least in relation to *Barbourisia* and *Rondeletia*) requires data from some additional taxa for outgroup comparison. The taxa chosen are the Beryciformes, including the Stephanoberyciforms, with data from Zehren (1979). These characters are considered first.

1. Pelvic fins. All cetomimids lack pelvic fins and pelvic girdles. Pelvic fins and girdles are present in *Rondeletia* and *Barbourisia*, as well as all beryciforms examined by Zehren (1979). The absence of pelvic fins and girdles is a synapomorphy defining the family Cetomimidae.

2. Pleural ribs. All cetomimids lack pleural ribs. Pleural ribs are present in *Rondeletia* and *Barbourisia*, and in all Beryciformes (Zehren, 1979). The absence of pleural ribs is a synapomorphy for the Cetomimidae.

* Pyloric caeca. Pyloric caeca are not found in cetomimids. The number of pyloric caeca in *Barbourisia* ranges from 9-14; 6 are found in *Rondeletia*. No data on pyloric caeca in the Beryciformes are available (Zehren, 1979; Ebeling & Weed, 1973; Woods & Sonoda, 1973). Whether the presence or absence of pyloric caeca is derived cannot be determined with the available data and the character is not utilised in the phylogenetic analysis.

* Medial gill tooth plates arch 4. All cetomimids lack tooth plates on the medial face of the fourth gill arch, whereas these elements are present in both *Barbourisia* and *Rondeletia*. However no data are available on the condition in other beryciform families (Zehren, 1979) and the derived state cannot be determined with the present data.

* Basibranchial tooth plates. One other feature distinguishes all cetomimids from *Rondeletia* and

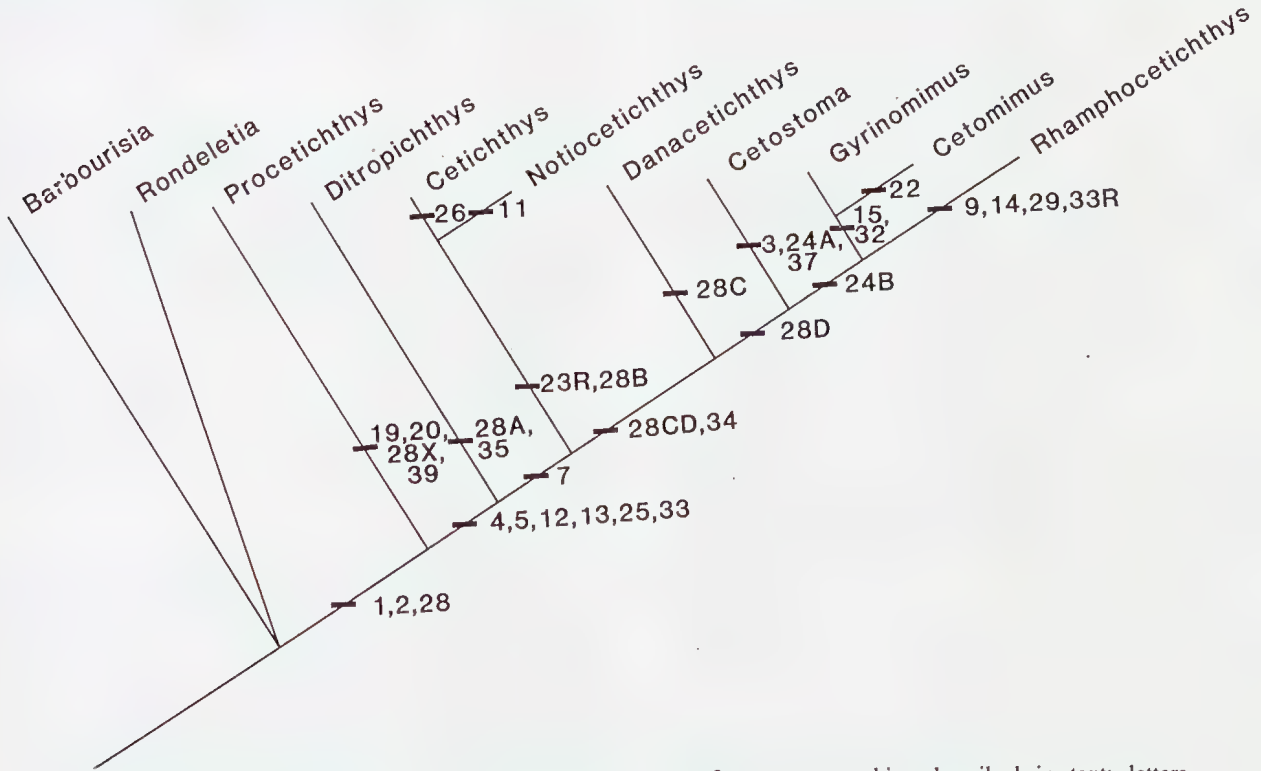

Fig.29. Relationships of the cetomimid genera; numbers refer to apomorphies described in text; letters A-D refer to different states in a transformation series, R to reversals.

Barbourisia. These latter two genera lack basibranchial tooth plates, which are present in all cetomimids. However basibranchial tooth plates are present in the Polymixiidae, Berycidae, Monocentrididae and some Holocentridae and absent in all other beryciforms (Zehren, 1979). The available data do not allow determination of the derived state for this character.

3. Dorsal and anal finray number. The number of cetomimid dorsal and anal finrays ranges from 11 to 37 and can be divided into only two clear states, 11 to 22 and 26 to 37. With both *Rondeletia* and *Barbourisia* falling in the lower range, the higher number is considered the derived state and is autapomorphic for the monotypic *Cetostoma*.

In *Cetostoma* and *Ditropichthys* there are consistently two to four more dorsal rays than anal rays (in *Ditropichthys* the ranges do not overlap), while in all other cetomimid genera the number of dorsal and anal rays are equal or vary inconsistently by one or two rays. While *Barbourisia* always has more dorsal than anal rays, in *Rondeletia* they are equal in number or almost so and the derived state cannot be determined on present evidence for this character set.

4. Pectoral finray number. The number of cetomimid pectoral rays ranges from 15 to 24, with the only clear break between 15 in *Procetichthys* and 17 to 24 in all other genera. The higher number results from the presence of small ventral rays which decrease in size ventrally; these tiny ventral rays are not present in *Procetichthys*. *Rondeletia* and *Barbourisia* have fewer rays than any cetomimid and lack tiny ventral pectoral rays. The higher pectoral ray number is considered derived.

5. Principal caudal finray number. The number of principal caudal rays in the Cetomimidae ranges from ten (five dorsal plus five ventral rays) to 19 (10+9). With 19 principal rays in *Rondeletia* and *Barbourisia* (as well as most pre-perciform fishes), the reduced number of caudal rays is considered derived and found in all cetomimid genera except *Procetichthys*. The caudal fin is distinctly forked in *Procetichthys* (Fig. 10), and moderately to weakly forked in *Rondeletia* and *Barbourisia*. In almost all other cetomimid specimens, the caudal rays are weak and easily broken, with no caudal fins complete. None of the fins appear strongly forked, however, and seem rounded, truncate, emarginate or weakly forked, suggesting the caudal is not used strongly in propulsion.

6. Total vertebral number. The total number of cetomimid vertebrae ranges from 38 to 59 while in the outgroups, *Rondeletia* has 24 to 27 (n = 19) and *Barbourisia* has 40 to 43 (n = 15). Although the variation is almost continuous within the family Cetomimidae, *Ditropichthys*, *Cetichthys* and *Notocetichthys* clearly have low ranges with some specimens having less than 40 vertebrae, while *Cetostoma*, *Gyrinomimus* and *Cetomimus* have ranges that include some specimens with more than 50 vertebrae. The low range is considered primitive and the intermediate values of three genera are included in the derived state with respect to *Rondeletia* and *Barbourisia*.

7. Preanal vertebral number. The cetomimid preanal vertebral number ranges from 20 to 40, with only *Procetichthys* and *Ditropichthys* having the low number of 20 (range 20 to 24). The range in the other cetomimid genera is 23 to 40; *Rondeletia* and *Barbourisia* have nine to 19 preanal vertebrae. The higher number of preanal vertebrae is considered derived. The extensive range of total vertebral numbers in *Gyrinomimus* and *Cetomimus* is correlated with the variation in preanal vertebrae.

Procetichthys and *Cetostoma* have a higher number of anal vertebrae than all other cetomimids (with that of the latter presumably correlated with the higher number of dorsal and anal rays). *Rondeletia* has fewer than 16 anal vertebrae and *Barbourisia* has more than 20; the derived state cannot be determined.

8. Lateral line organ number. The number of lateral line neuromasts, one fewer than the number of lateral line pores in those genera with a lateral line canal, ranges from eight to 86 in the cetomimids, with the higher number of 31 to 86 found in *Rhamphocetichthys* and *Procetichthys*. All other cetomimid genera have eight to 24 neuromasts. The number of neuromasts in *Barbourisia* and *Rondeletia* ranges from 14 to 32, with the number in *Rondeletia* being the number of vertical rows of neuromasts. The higher number of neuromasts is considered derived in the Cetomimidae. The number of lateral line neuromasts is not related to vertebral number.

The lateral line consists of vertical rows of neuromasts in *Procetichthys* and *Rhamphocetichthys* and a canal with single neuromasts covered by a bridge of skin in all other cetomimid genera. Since *Rondeletia* has vertical rows of neuromasts and *Barbourisia* has a lateral line canal, the derived state in the Cetomimidae cannot be determined.

9. Length of snout. The only measurements considered for character analysis were those eight (of 22; Appendix Table 9) for which at least one genus had a range outside all other genera. These eight measurements were taken on six specimens of *Rondeletia* and five of *Barbourisia* (see Materials and Methods).

The snout length ranges from 7.9 to 19.5% SL in the Cetomimidae. The long snout of *Rhamphocetichthys* is distinctive within the cetomimids. *Rondeletia* has a longer snout than *Barbourisia*, thus putting into question which state is derived. However the snout of *Rhamphocetichthys* is elongate and pointed with the upper jaw overhanging the lower, unlike the rounded jaws of all other taxa examined, including *Rondeletia*, and is considered derived.

10. Width of head between eyes. The width between the eyes ranges from 3.2 to 21.6% SL in the cetomimids, with those of *Barbourisia* and *Rondeletia* ranging from 11.8 to 19.9%. The eye widths of *Cetostoma* and *Rhamphocetichthys* were the narrowest measured and are considered derived.

* Lengths of snout to dorsal, dorsal base and anal base. The short snout to dorsal fin origin distance and long dorsal and anal fin bases of *Cetostoma* are outside the ranges of all other taxa measured including *Barbourisia* and *Rondeletia*, are correlated with the high dorsal and anal fin counts and are considered derived. These characters were not utilised in the computer programme, because to do so would in effect be weighting what appears to be a single feature, the increased number of dorsal and anal fin rays (character 3).

* Length of anus to anal origin. The anus is further forward of the anal fin origin in *Procetichthys*, *Cetichthys* and *Notocetichthys* (distance = 5.0-9.9% SL) than in all other cetomimids (0.6-4.3% SL). The outgroup genera display both character states, with the measurements of *Rondeletia loricata* extending into the range of the higher values and the single specimen of *R. bicolor* with an advanced anus (7.2% SL). The softness of the tissue and poorly defined finbases in this genus make the measurements more subjective than most. The derived state is not clear and the character is not utilised in the analyses.

11. Length of copular tooth plate. The length of the copular tooth plate in cetomimids ranges from 0.9 to 15% SL. The negative allometric growth of this element results in the high percentage SL for *Danacetichthys* and some small specimens of *Cetichthys* and precludes the separation of the long copular tooth plate of *Cetostoma* as a distinct character state. However the very short tooth plate in *Notocetichthys* is clearly outside the range of all other genera measured. A copular tooth plate is lacking in both *Barbourisia* and *Rondeletia* and the polarity of the two states of tooth plate length cannot be determined by outgroup comparison. However, the negative allometry apparent in two genera, with a relatively longer tooth plate present in the smallest specimens, is ontogenetic evidence that the short copular tooth plate of *Notocetichthys* is derived.

* Ratio of copular tooth plate length/width. The ratio of copular tooth plate length/width displays two character states, with the long, narrow plates of *Procetichthys* and particularly *Cetostoma* having ratios far exceeding those of all other taxa measured. However the derived state cannot presently be determined, due to the absence of the plate in *Barbourisia* and *Rondeletia* and the lack of any clear indication of allometry.

12. Nasal organ development. The nasal organ of cetomimids is well developed, elongate and has more than 30 lamellae in *Procetichthys*, whereas it is reduced, short and round with none to ten lamellae in all other cetomimids (Fig. 1). In *Barbourisia* the nasal organ is fully developed with up to 30 lamellae and in *Rondeletia* it is moderately large and elongate with 13 to 18 distinct lamellae. The reduced state is considered the derived condition in cetomimids.

13. Eye lens development. A well-developed lens is present in the eye of the outgroup genera *Rondeletia* and *Barbourisia* and is retained as a primitive condition only in the cetomimid genus *Procetichthys*. No lens is present in any other cetomimid over 100 mm SL, but is present or reduced in the small specimens (34-54 mm) of *Danacetichthys*. Ontogenetic reduction and loss of the eye lens is considered the derived state in cetomimids.

14. Cephalic laterosensory system. In *Barbourisia* and *Rondeletia* and all cetomimid genera except *Rhamphocetichthys*, the laterosensory system on the head consists of a series of canals covered by skin that is pierced by large pores. In *Rhamphocetichthys* a series of widely spaced free papillate neuromasts are joined by underlying nerves, in the approximate position of the canals of the other genera. The papillate neuromast system is considered autapomorphic for the monotypic *Rhamphocetichthys*.

15. Supraorbital head canal. The supraorbital head canal is joined to the main head canal in *Barbourisia* and *Rondeletia* and all cetomimid genera except *Gyrinomimus* and *Cetomimus* and questionably *Cetostoma* and *Danacetichthys*, where they are broken into two separate canals. The discontinuous condition is considered derived.

16. Dorsal head canal pore number. The number of pores in the dorsal canal of the head (the supraorbital canal plus the main canal) ranges from eight to 12 in the Cetomimidae with two states: 8-9 and 10-12. The number of dorsal pores in both *Barbourisia* and *Rondeletia* is eight and the higher number in cetomimids is considered derived.

17. Infraorbital head canal. The infraorbital canal is distinctly separate from the supraorbital canal in all cetomimid genera except *Cetichthys*, in which they are joined, and *Ditropichthys*. In *Ditropichthys* the canals are partially joined (a neuromast is present between the two pores, but the covering skinbridge has been lost). In both *Barbourisia* and *Rondeletia* the two canals are joined. Separate canals are considered derived in cetomimids.

The cetomimid number of infraorbital pores ranges from eight to ten, but does not fall into distinct classes; *Rondeletia* has seven infraorbital pores and *Barbourisia* has ten.

18. Last infraorbital neuromast. The last (counting from anteriorly) infraorbital neuromast and two adjoining pores are displaced anterodorsally, so they are not continuous with the rest of the infraorbital canal, in five cetomimid genera. In all other genera plus *Barbourisia* and *Rondeletia* the canal is continuous; the displaced condition is considered derived for cetomimids.

19. Nasal organ infraorbital canal connection. A small pore joins the posterior nasal cavity with the anterior circumorbital canal in *Procetichthys*. The connection is considered autapomorphic for this monotypic genus, as it was not found in any other taxon examined. However two pores are present in the posterior wall of the nasal cavity at the end of the raphe in *Rondeletia*, where they lead to an organ of unknown function, briefly described by Tominaga (1970). The pores in the two taxa are not considered homologous, as the organ behind the nasal cavity in *Rondeletia* is not apparent in *Procetichthys*.

20. Jaw tooth spacing. In *Barbourisia*, *Rondeletia* and all cetomimid genera except *Procetichthys*, the jaw teeth are closely set, with the tooth bases almost touching, or at least less than the basal width of a tooth apart (Fig. 2). The jaw teeth of *Procetichthys* are very widely spaced in one to two uneven rows, with the space between teeth greater than the basal tooth width (Fig. 2a), and this is considered the derived condition.

21. Jaw tooth rows. In *Barbourisia*, *Rondeletia* and most cetomimids the jaw teeth are organised in approximately diagonal rows across the oral surface of the jaws (Fig. 2b, d-f). In *Danacetichthys* and most species of *Gyrinomimus* the jaw teeth are set in distinct longitudinal rows down the length of the jaws (Fig. 2c). In only two undescribed species of *Gyrinomimus* the early teeth formed in juveniles are in

diagonal rows, while teeth added later in life are in longitudinal rows (Paxton, ms). Both outgroup comparison and ontogenetic evidence support the consideration of longitudinal rows as the derived state.

22. Vomer. The vomer displays a variety of conditions, from edentate in *Rondeletia* and *Notocetichthys*, to having two teeth in *Procetichthys*, to having numerous teeth in other genera; the shape of the tooth patch varies from triangular to rectangular, trapezoidal, elipsoidal, oval and round with shape and number of teeth defying objective division into discrete character states. However in *Cetomimus* the vomer projects distinctly ventrally into the oral cavity as a hemispherical dome, becoming more pronouncedly domed in larger individuals. In all other genera including *Barbourisia* and *Rondeletia*, the vomer is flat or only very slightly domed, and the domed vomer of *Cetomimus* is considered derived. The vast majority of species of *Cetomimus* have a vomer that is round in outline, in contrast to the rectangular to oval vomer seen in *Gyrinomimus*.

23. Palatine teeth. The outgroup genera *Barbourisia* and *Rondeletia* and the cetomimids *Cetichthys* and *Notocetichthys* lack palatine teeth. The presence of palatine teeth in all other cetomimid genera is considered derived.

* Ectopterygoid teeth. The ectopterygoid of *Rondeletia* is toothless, whereas the ectopterygoid of *Barbourisia* has a long tooth plate extending to the rictus. All but two cetomimid genera share the long toothplate with *Barbourisia*, whereas that tooth plate is very short in *Cetichthys* and absent in *Notocetichthys*. While one of the states should define a lineage within the cetomimids, the polarity of evolution cannot be determined from the two outgroup genera.

* Copular tooth plate(s). Three separate basibranchial tooth patches are present in *Cetostoma*, whereas a single basibranchial tooth patch is found in all other cetomimids. As both *Barbourisia* and *Rondeletia* have edentate basibranchials, the derived condition for the number of cetomimid basibranchial tooth plates cannot be determined from present data.

24. Fourth gill slit. The fourth gill arch is free, with a large gill slit extending above the angle behind the fourth arch of *Barbourisia*, *Rondeletia* and the cetomimid *Procetichthys*. In most other cetomimids the fourth gill slit is reduced to an opening behind the ventral arm of the fourth arch; in *Cetostoma* the fourth gill slit is further reduced to a small tubular opening behind the angle of the fourth arch (state 24A). In *Rhamphocetichthys*, *Gyrinomimus* and *Cetomimus* the fourth slit is completely closed, with only three free gill arches, and this is considered the most derived condition (state 24B). The unique condition in *Cetostoma* is considered a separate state as part of a transformation series.

25. Pseudobranch. A pseudobranch on the inside of the gill cover is present in *Barbourisia*, *Rondeletia* and the cetomimid *Procetichthys*. Its absence in all other cetomimids is considered derived. With this and the other characters of loss, there is no evidence that the loss occurred more than once.

26. Arch 1-3 holobranchs. The holobranchs or gill filaments of the first three gill arches are well developed and closely set in *Barbourisia*, *Rondeletia* and all cetomimids except *Cetichthys* (Fig. 3). In *Cetichthys* the holobranchs are very reduced and far separated (Fig. 3b) and this is considered the derived condition. In cetomimids the amount of the dorsal arm of the first gill arch bearing holobranchs varies from more than 50% to 0, but the variation is a continum and states are not defined.

27. Arch 4 holobranchs. The holobranchs of the fourth gill arch are well developed, closely set and at least half the length of those on the first arch in the outgroup genera *Barbourisia* and *Rondeletia* and most cetomimids. In *Cetichthys* the holobranchs of the fourth arch are as reduced and widely spaced as those of the first arch. In *Cetostoma*, *Cetomimus* and most species of *Gyrinomimus*, the filaments are closely spaced but reduced in length to less than a quarter of those on the first arch, in some species being almost invisible. The reduced conditions are considered derived.

28. Gill raker form. In *Barbourisia* and *Rondeletia*, the gill rakers are elongate and slightly flattened in shape, typical of rakers in most fishes. In *Procetichthys*, gill rakers have been replaced by individual isolated teeth (Fig. 3a). In *Ditropichthys* the gill rakers are club shaped (Fig. 3c), in *Cetichthys* and *Notocetichthys* low, toothed knobs (Fig. 3b), in *Danacetichthys* domed, rounded tooth plates (Fig. 3d) and in the other four genera flat tooth plates that often fuse with increasing age to form an unbroken patch of teeth (Fig. 3e-h). With elongate the primitive outgroup condition, the other forms are considered a transformation series from club shaped (state 28A), to low knobs (state 28B), to domed plates (state 28C) through to flat plates (state 28D); the isolated teeth of *Procetichthys* are considered derived (state 28X), but not a stage of the transformation series.

29. Arch 2-3 gill "rakers". Gill rakers or their equivalent are present on the second and third gill arches of the outgroup genera *Barbourisia* and *Rondeletia* and all cetomimids except *Rhamphocetichthys*, where their loss is considered derived. The loss of gill tooth plates on the fourth gill arch is usually correlated with the closure of the fouth gill slit, and is not distinguished as a separate character.

30. Medial gill "rakers". In *Barbourisia*, small gill rakers are present on the medial faces of all four gill arches. In *Rondeletia* gill rakers in the form of small tooth plates are present on the medial faces of arches two to four (but not arch 1). Tooth plates are present on the medial faces of arches one to three in four cetomimid genera and absent in all or most species in five genera. The loss of these medial elements from arches two to three is considered derived in the Cetomimidae.

31. Ventral pharyngeal tooth plate. Paired ventral pharyngeal tooth plates are present on the fifth ceratobranchial of both *Barbourisia* and *Rondeletia* (very small in *Rondeletia*) and three cetomimid genera. The loss of these tooth plates in six cetomimid genera is considered derived.

* Lateral line form. The lateral line of *Barbourisia* is a

deep canal with the overlying skin pierced by small pores and supported by scales in the medial wall of the lateral line canal. In *Rondeletia* the lateral line is a series of vertical rows of papillate neuromasts, without underlying scales. Vertical rows of neuromasts with underlying scales are present in two cetomimid genera, with the rest having a shallow or deep canal, large pores and supporting scales. The two character states cannot be polarised on the basis of the outgroup condition.

32. Lateral line scales. In seven cetomimid genera the lateral line scales lie flat in the medial wall of the lateral line canal and are round-oval or rectangular in shape with smooth margins (Fig. 5b). In *Gyrinomimus* and *Cetomimus* the scales are elongate and curved, with the dorsal and ventral edges curved up the sides of the lateral line canal to support the overlying skin; the dorsal and ventral margins have one to many projections (Fig. 5c). *Rondeletia* lacks lateral line scales, while the lateral line scales of *Barbourisia* are curved with dorsal and ventral projections. However these projections are double and supported by numerous cross struts (Fig. 5a). The curved scales of *Barbourisia* do not appear homologous with those of *Gyrinomimus* and *Cetomimus*. While the flat versus curved states cannot be polarised on the basis of the outgroup genera, they are polarised due to their correlation with numerous other derived states in *Gyrinomimus* and *Cetomimus* (Table 10). The different states are objective and easy to define, suggesting a major evolutionary change.

33. Cavernous tissue. Cavernous tissue is lacking in both outgroup genera *Barbourisia* and *Rondeletia* and the cetomimids *Procetichthys* and *Rhamphocetichthys* (although a slight indication is present over the lateral line scales of the latter genus). In all other cetomimid genera cavernous tissue is present at least in bilateral areas anterodorsal to the anus. The presence of cavernous tissue is considered the derived state. In *Ditropichthys* and some species of *Gyrinomimus* and *Cetomimus*, cavernous tissue is also present in at least one other area (fin bases, lateral line, caudal peduncle, abdomen). While cavernous tissue at areas other than close to the anus might be considered a further derived state in a transformation series, it is not done so here because the additional areas are different in different taxa and not all species of the latter two genera have the additional tissue.

34. Subpectoral organ. A subpectoral organ is discernible in five cetomimid genera (only in some species of two of these) and absent in the other four cetomimid genera and *Barbourisia* and *Rondeletia*. The presence of a subpectoral organ is considered the derived state.

35. Paired abdominal ridges. In *Ditropichthys* two flaps of skin extend from near the pectoral base to the anus, supported internally by ridges most developed posteriorly in the ventral wall of the abdomen. No such ridges or paired flaps are present in any other cetomimid or *Barbourisia* and *Rondeletia*. The paired ridges are considered autapomorphic for the monotypic *Ditropichthys*. A single, weak, midventral ridge is present in a few cetomimids and is similar to the mid-dorsal ridge found in many cetomimids. The weak single ridges are not characterised because in a number of cases they seem to be dependent on preservation quality.

36. Anal lappets. Long flaps of skin supported by internal scales hang over the anal fin base in *Ditropichthys* and *Cetostoma*. Separate anal lappets with internal scales are present in *Rhamphocetichthys* and some species of *Gyrinomimus*, while a single lappet without a scale is present in one of the two species of *Cetichthys*. The other four cetomimid genera and both outgroup genera *Barbourisia* and *Rondeletia* lack anal lappets. As the different types of lappets do not appear to represent a clear transformation series, they are combined into a single derived character state. Although the number of lappets and whether they are separate or joined vary among the five cetomimid genera, their position over the anal fin and the usual presence of scales are the basis for considering them homologous.

37. Anal fin membrane. The membrane joining the last ten anal rays is voluminous and curtain like only in the monotypic *Cetostoma* (Fig. 21), where it is considered autapomorphic; it does not occur in any other cetomimid or the outgroup genera *Barbourisia* and *Rondeletia*.

38. Stomach pigment. The wall of the stomach is dark brown in all cetomimids except *Rhamphocetichthys*, where it is light brown and *Procetichthys* and *Cetostoma*, which lack stomach pigment. As both *Barbourisia* and *Rondeletia* have darkly pigmented stomachs, the complete lack of pigment is considered derived within the cetomimids.

39. Peritoneal pigment. The peritoneal lining is light brown in *Cetostoma* and dark brown in all other cetomimids except *Procetichthys*, which lacks peritoneal pigment. The peritoneal lining of *Barbourisia* is dark, that of *Rondeletia* is light brown. The lack of pigment is considered derived within the Cetomimidae.

Discussion. The 39 character sets (Table 10) were analysed by the computer programme PAUP version 2.4 (Swofford, 1985) to produce phylogenies based on parsimony, with the minimum number of evolutionary steps. *Rondeletia* and *Barbourisia* were combined as a single outgroup. The data matrix was manipulated once: characters with two states in one genus were changed from missing to derived for a second analysis. The two runs produced a total of nine trees (one and eight trees respectively).

A combination of the nine trees indicates that unresolved problems involve the relationships of *Cetichthys* with *Notocetichthys* and of the five most derived genera. The cladogram presented as a working hypothesis (Fig. 29) comes closest to two trees (one in each analysis), the only difference being the order of the genera *Cetostoma* and *Rhamphocetichthys*, as discussed below.

The monophyly of the family Cetomimidae is supported by three synapomorphies relative to *Barbourisia*, *Rondeletia* and other families of the Beryciformes, the absence of pleural ribs and pelvic fins and the presence of gill rakers in some form other than elongate and flattened. The establishment of *Procetichthys* as the primitive sister group of all other cetomimids is one of the most unequivocal nodes in the cladogram. The monophyly of the remaining cetomimid genera (here considered a

subfamily) is supported by five synapomorphies and the monotypic *Procetichthys* is defined by four autapomorphies.

The genus *Ditropichthys* is placed as the primitive sister group of the remaining seven genera in all analyses, although only one synapormorphy, the higher number of preanal vertebrae (character 7), supports the monophyly of the other genera. The monotypic *Ditropichthys* is defined by the autapomorphic features of paired abdominal ridges and gill rakers in the form of toothed clubs (characters 28A, 35).

The relationship of *Cetichthys* and *Notocetichthys* was not resolved in the computer analyses. In some phylogenies they were in a monophyletic line defined by the gill raker form of toothed knobs (character 28B), while in others the monotypic *Notocetichthys* was separate and more primitive, defined by the single autapomorphy of a short copular tooth plate (character 11). The most parsimonius cladogram includes these two genera in a monophyletic line that is also defined by the loss of palatine teeth (character 23R). This latter synapormorphy is a reversal of the derived condition for the family Cetomimidae of palatine teeth present. *Cetichthys* is defined by the synapomorphic feature of reduced holobranchs.

The monophyly of the remaining five genera is supported by gill raker form (character state 28C,D) and the presence of a subpectoral organ in at least some species of each genus (character 34); every computer analysis placed them in monophyly. However the relationships of each to the other is ambiguous. Only the sister group relationship of *Gyrinomimus* and *Cetomimus* was recognised in all analyses, with the line defined by the form of the lateral line scales (character 32). The shape of the vomerine tooth plate (character 22) defines *Cetomimus*. *Gyrinomimus* lacks a synapomorphic character, as the distinctive longitudinal rows of elongated teeth (character 20) are also found in *Danacetichthys*.

The relationships of the other genera are open to question. Both *Cetostoma* and *Rhamphocetichthys* are highly derivative forms, with each monotypic genus defined by three or four autapomorphies.

The hypothesis chosen for the relationships of the five genera (Fig. 29) is identical to one of the nine trees produced and is supported by the two characters with multiple state changes, gill raker form (28) and fourth arch gill slit (24). *Danacetichthys* is placed as the sister group of the other four genera due to the unique, intermediate form of the gill arch tooth plates (Fig. 3d). This genus is known only from six juvenile specimens. However *Danacetichthys* is not merely the juvenile form of one of the more than ten species of *Gyrinomimus*. Although the jaw teeth are similar to those of *Gyrinomimus*, none of even the smallest specimens of *Gyrinomimus* have gill tooth plates the same as those of *Danacetichthys*, the fourth gill slit is always closed in *Gyrinomimus* and the lateral line scales have dorsal and ventral projections.

Consideration of *Cetostoma* as the sister group of the other three genera is supported by the reduction and closure of the fourth gill slit (character 24). None of the other solutions allowed each line to be defined by at least one synapomorphy. The chosen hypothesis (Fig. 29) is similar to the single tree generated in the first analysis (where characters with two states in one genus were considered missing), differing only in the reversed order of *Cetostoma* and *Rhamphocetichthys*. Such a solution, with *Rhamphocetichthys* as the primitive sister group of the other three genera, requires a reversal of character 24, a reopening of the fourth gill slit in *Cetostoma*, and is rejected because it is less parsimonius. The only reversal evident in the present solution is the loss of cavernous tissue in *Rhamphocetichthys*, and this reversal is required in every tree.

Some comments about the analysis and resulting phylogeny are warranted. One feature restricted to and widely distributed within the family Cetomimidae proved of less value in ascertaining generic relationships than expected. The distribution of anal lappets (character 36) does not define any of the hypothesised monophyletic lines within the family. As lappets are absent in *Procetichthys* and present in *Ditropichthys*, they presumably evolved in the ancestor to *Ditropichthys*. The anal lappets display a labile evolutionary picture, being fully developed and completely joined in *Ditropichthys*, reduced to one in one species of *Cetichthys* and lost in the other species, as well as in *Notocetichthys*, fully developed and partially joined in *Cetostoma*, as separate elements in *Rhamphocetichthys* and some species of *Gyrinomimus* and presumably independently lost in *Danacetichthys*, some *Gyrinomimus* and *Cetomimus*. A classification that required fewer evolutionary changes for this feature would result in many more reversals for other characters. Perhaps the evolutionary labileness will be more explicable when the function(s) of anal lappets are understood.

The characters utilised in the present analysis do not include the less labile osteological features. Clearly further characters and analyses are required to resolve some areas and test the present hypothesis of relationships.

This synopsis recognises six monotypic genera. Two factors influenced the subjective decisions of what level to draw generic limits. The genera *Gyrinomimus* and *Cetomimus* each contain more than ten species. Further, the few available specimens of both *Danacetichthys* and *Rhamphocetichthys* suggest that more than one species may be involved. Finally the fact that the majority of species are known from fewer than ten specimens suggests that more species will be discovered in the future.

Biology

Sight. The eyes of most cetomimids grow very little with increasing size, and with the exception of *Procetichthys*, do not exceed 2.0 to 2.5 mm diameter. The same holds true for female ceratioid anglerfishes, another bathypelagic group (Bertelsen, 1951). The lack of a lens in most adult whalefishes indicates that image formation is not possible, although Munk (1965) concluded that light perception

might be possible even in the most degenerated eyes. With a well-formed lens, the eye of *Procetichthys kreffti* presumably is capable of both light detection and image formation, as are the eyes of at least young *Danacetichthys galathenus*.

The remnants of a degenerating lens have been found in two of the smallest specimens of *Cetostoma regani* (40.7 and 50.2 mm), but in other specimens 39.7 mm and over the lens is gone. Similar remnants are present in a 39.5 mm specimen of *Cetomimus* sp. F, but not in other specimens of the genus 45.7 mm and over. No remnants have been discernible in any of the other five genera, including specimens of *Ditropichthys* as small as 26.8 mm and *Gyrinomimus* 51.0 mm. The presence of lens remnants supports the suggestion of Munk (1965), that the eyes are fully differentiated and functional in juvenile whalefishes and degenerate with age. The degeneration presumably would be related to the lack of light in the bathypelagic depths inhabited by adult whalefishes. No specimens smaller than 25 mm have ever been taken.

Olfaction. Marshall (1967) surveyed the olfactory organs of bathypelagic fishes and found two different types of nasal organs. In bathypelagic representatives of a few families (Serrivomeridae, Nemichthyidae, Macrouridae), both males and females have reduced nasal organs. The majority of bathypelagic species studied (all but one family of ceratioid angler fishes, Gonostomatidae) are sexually dimorphic, with males having large nasal organs and females reduced nasal organs and associated areas of the brain. To this list can now be added Eurypharyngidae (Gartner, 1983), Saccopharyngidae (Nielsen & Bertelsen, 1985) and Monognathidae (Bertelsen & Nielsen, 1987). In contrast, almost all mesopelagic and deep benthic fishes have moderate or large nasal organs in both sexes. As all examined cetomimids have been females, all whalefishes except *Procetichthys kreffti* are thus typical bathypelagic fishes with greatly reduced nasal organs in females.

Male cetomimids have yet to be discovered. Gosline (1971:135) suggested, without elaboration, that megalomycterids may prove to be the macrosomatic males of cetomimids. This suggestion will be considered in detail in a future paper on the osteology of the Cetomimidae. Suffice it to say that, while appealing, identification of megalomycterids as male cetomimids would appear to be refuted by, among other features, determination of the 34.5 mm holotype of *Megalomycter teevani* as a female (Myers & Freihoffer, 1966:195).

The limited development of weak olfactory lamellae in some specimens of *Cetomimus* and *Gyrinomimus* (Fig. 1j,k) appears to be size related, as the smallest specimens lack any indication of lamellae. The loss of olfactory acuity presumed by the reduction and loss of lamellae (not necessarily a valid assumption, see for instance Thiesen *et al.*, 1980) which parallels the loss of sight in the dark bathypelagic environment is explicable if food in this environment does not give off many odours. Marshall (1967:69) concluded that in most bathypelagic species "...the olfactory organs and associated brain centres are so reduced that they are most unlikely to help in the finding of food." The loss of both sight and smell is apparently compensated for in cetomimids by one of the widest lateral line systems known in fishes. The lack of a cavernous lateral line in *Procetichthys kreffti* is associated with both a large nasal organ and presence of an eye lens. However *Rhamphocetichthys savagei* lacks a large nasal organ, eye lens and cavernous lateral line.

Mechanoreception. Coombs *et al.* (1988) and Webb (1989) have surveyed the distribution and variety of lateral line systems in fishes. The cetomimids are richly endowed with both wide lateral line canals and large numbers of papillate superficial neuromasts. Coombs *et al.* (1988: 586) point out that it is not unusual to find these two features in combination, and that their evolution may be favoured in low-noise environments. The deep sea cetomimids appear to be a particularly striking example of this correlation.

The head canal pattern of cetomimids is a variation of the standard teleost pattern. The loss of head canals in *Rhamphocetichthys* is combined with their replacement by lines of superficial neuromasts, an event which has occurred independently in many fish groups (Coombs *et al.*, 1988: Fig. 22.14). The loss of the main trunk canal and its replacement by vertical rows of superficial neuromasts, the trunk accessories, has occurred independently in *Procetichthys* and *Rhamphocetichthys*. These monotypic genera are known from one and four specimens respectively and nothing is known of their biology that is different from the other whalefishes to correlate with this lateral line specialisation.

Of the four major head canal types identified in teleosts (Webb, 1989), cetomimids have widened canals without bony walls or roofs (although the orientation of the cupula in the canal, one of the defining characteristics of canal type, has not been determined). While the head canals of *Procetichthys* are relatively the narrowest of the family (Fig. 4), they are covered in skin, not bone.

Primary variations in the head canals of the lateral line system include whether the supraorbital canal is continuous with or separate from the main canal, whether the infraorbital canal is separate from or joined to the main canal and whether the last (posterior) neuromast and its associated pores of the infraorbital series is continuous with the series or displaced anterodorsally. According to the evolutionary relationships proposed in the previous section, each of these three evolutionary events occurred only once in the family. Secondary variations include differences in the numbers of neuromasts and pores in each canal and in the numbers of superficial neuromasts in various lines. Each of these features may vary in a single species of cetomimid.

Three primary differences are apparent in the main trunk canal, the most fundamental being the replacement of the trunk canal with vertical accessory lines of superficial neuromasts in *Procetichthys* and *Rhamphocetichthys* mentioned above. The remaining genera have two basic types of trunk canal which are influenced by the type of lateral line scales in the floor of the canal. In all genera except *Gyrinomimus* and *Cetomimus*, the lateral line scales are flat and two dimensional; the sides of the lateral line

canal are unsupported. In many taxa the "canal" consists of very narrow skinbridges barely covering the neuromast and not nearly the width of the scale (Fig. 20). This shallow condition of the lateral line may be related primarily to size; the largest specimens of at least *Cetichthys parini* have more cavernous lateral line canals, as the longest specimens also have more flesh on the head and body.

In *Gyrinomimus* and *Cetomimus* the lateral line scales have lateral extensions which support the lateral walls of a deeper and more cavernous trunk canal (Fig. 5c). These scales not only provide support for the lateral canal wall, but provide wide anchoring points for the roof of the canal. With such anchoring points and lateral walls, the diameter of the canal is thus restricted at the scale and overlying neuromast, in relation to the rest of the canal. Such restriction will increase the velocity of fluid flow past the cupula and increase the receptor response, while the increased volume of fluid in the widened canal increases sensitivity of the neuromasts (Denton & Gray, 1988). However the functional significance of the flaps that partially close off the posterior pores and the median keel on the posterior portions of the canal roof, both of which are most developed in *Gyrinomimus* and *Cetomimus*, has yet to be established.

The highly developed lateral line system of whalefishes is clearly the primary sensory system of these bathypelagic fishes, with both sight and olfaction systems reduced in almost all taxa. Increased sensitivity of the trunk canal presumably accrues with the greater development of a cavernous canal (increased canal depth) with growth. However the size at which this becomes most pronounced, at least in *Cetichthys parini*, is more than 150 mm SL, far beyond the size at which the eye lenses have degenerated. The extreme development of a cavernous trunk canal thus does not exactly correspond to the loss of the eye lens, but does provide an extensive sensory receptor system in adult whalefishes. Such a system must provide for the detection of prey, predators and conspecifics for reproduction. Neither the body shape nor fin development are indicative of rapid swimming in whalefishes (see below), that might jam a sensitive system. The extensive development of wide canals and superficial neuromasts provides the slow-swimming cetomimids with information about the quiet bathypelagic environment.

Respiration. Marshall (1960:171) has demonstrated the considerable reduction in organ systems in bathypelagic fishes when compared to mesopelagic species, including the number and extent of gill filaments. Marshall (1960) related this economy of form with increasing depth to the decreasing amount of available food. An extreme reduction in gill filaments is apparent in *Cetichthys* (Fig. 3b), the deepest dwelling of all cetomimids. Not enough closing net captures are available to determine exact depth ranges to correlate with total gill lamellae of other species. The great reduction in gill lamellae of *Cetichthys* may be related to the increased oxygen carrying capacity of deeper, colder water; or perhaps some type of cutaneous respiration supplements the oxygen supply from the degenerated gills.

Food and feeding. Ebeling & Cailliet (1974) correlated mouth size with living depth in the fish families Myctophidae and Melamphaeidae. They showed that the deeper-dwelling bathypelagic species of each family had larger mouths than the mesopelagic species. Such a generality does not appear to hold within the wholly bathypelagic family Cetomimidae. *Cetichthys* is the deepest dwelling cetomimid, yet the premaxillary length is not longer than that of some specimens of *Danacetichthys*, *Gyrinomimus*, *Cetomimus* or *Rhamphocetichtys* (Table 9), nor does *Cetichthys* apparently reach the maximum total length of any cetomimid to attain the largest absolute mouth. While the capability of taking the largest available meal presumably was the selective advantage resulting in the large mouths found in all cetomimids, extremes of depth apparently do not result in even larger mouth sizes.

Many of the features of whalefishes - exceptionally large mouth, lack of scales, ribs and pelvic fins, long abdominal region with posterior dorsal and anal fins and anus, and weak pectoral girdle with unforked post-temporal - would be advantageous in taking large, single meals such as a large fish. More than 300 specimens were x-rayed, and only five had visible stomach contents. All were of the genus *Gyrinomimus* and had a single relatively large fish in the stomach. Four of these were dissected and in each case the stomach contents consisted of a single myctophid in good to excellent condition, with complete scales in three cases. Each stomach also had other items in good condition (a stomatopod larva; a broken salp barrel and two crustaceans; a salp complete with phronemid amphipod). Net feeding during death throes in the trawl is the most plausible explanation of these largely mesopelagic food items in the stomach (see Hopkins & Baird, 1975 for a review of net feeding in mesopelagic fishes). The size of the fishes ingested (50 mm, 70 mm, 39 mm) relative to the size of the whalefish (125, 150, 150 mm) indicates cetomimids are capable of ingesting fish prey up to almost half their standard length, but normally do not do so.

Few cetomimids contained identifiable stomach contents (only those with obviously distended stomachs were dissected), presumably due to the scarcity of food at bathypelagic depths or regurgitation in the net. A total of 14 specimens representing five genera, including eight specimens of *Cetostoma regani*, contained recognisable stomach contents. All of the stomach contents were crustaceans, ranging from copepods to decapods. The dentition of whalefishes, small, closely-set teeth in all but *Procetichthys*, is presumably related to the crustacean diet, while the food of this latter genus is unknown.

The typical whalefish is heavy bodied with a large head, very poorly developed pectoral fin, low dorsal and anal fins, short and broad caudal peduncle and rounded to emarginate caudal fin. None of these features are correlated with rapid swimming and as hypothesised for many deep sea fishes, cetomimids are probably slow-swimming predators that lie in wait for prey to swim close to the large mouth. The only exception to this might be *Procetichthys*, which has a considerably larger pectoral fin, a distinctly forked caudal fin and a more compressed body. However the large number of superficial

neuromasts aligned in vertical rows on the trunk are not typically associated with fast swimming fishes and this species also is most likely a slow swimmer.

Age and growth. Assuming unbiased sampling and similar escape bahaviour in different taxa, there are clearly different maximum sizes in the different genera of cetomimids, with *Ditropichthys* attaining no more than 150 mm and *Gyrinomimus* reaching almost 400 mm. It is likely that the latter genus reaches larger sizes, as none of the examined specimens were reproductively mature. The best representation of size range is available for *Ditropichthys*, with 84 specimens known from 25 to 131 mm SL (Table 4). Allometric growth is apparent in a number of parameters, the most striking feature being the addition of fat and muscle in larger specimens, particularly in *Ditropichthys* and *Cetichthys*, resulting in heavier, deeper bodies. Specimens smaller than 40 mm are unknown for most taxa. No data are available for age estimates.

Reproduction. The vast majority of examined cetomimids have been immature. All examined specimens that were large enough to have gonads identifiable by observation up to 50 times magnification have been females. This has been confirmed by embedding and sectioning gonads of eight medium to large specimens representing five species in four genera. No indication of testicular tissue has been found.

Almost all of the ovaries examined have been filled with eggs 0.1 mm or less in diameter. The largest eggs seen are in the 236 mm holotype of *Procetichthys kreffti*, with eggs 1.9 to 2.0 mm in diameter. A 280 mm specimen of *Gyrinomimus andriashevi* (ISH 952/71) has eggs up to 1.3 mm in diameter, while the largest eggs of 75 dissected specimens of *Cetostoma regani* are 0.6 mm in diameter from a 204 mm specimen. All three of these fishes had smaller eggs in the ovaries, with the latter specimen having only a few 0.6 mm eggs and many eggs much less than 0.1 mm diameter. Five other specimens of *C. regani* had two eggs sizes in the ovary (0.1 mm and much less than 0.1 mm), as did the only specimen of *Ditropichthys storeri* (112 mm) with eggs greater than 0.15 mm (0.25 mm and less than 0.1 mm). At least some species of cetomimids appear to spawn more than once per lifetime, unlike the scenario that has been proposed for an increasing number of bathypelagic fishes. There is no evidence that cetomimids go through a nuptial metamorphosis involving the reduction in feeding and other systems that precedes a single spawning and then death, as proposed for the Anotopteridae, Paralepedidae, Notosudidae, Nemichthyidae, Saccopharyngidae and Monognathidae (Bertelsen & Nielsen 1987:167).

The great disparity in egg sizes found in a single ovary (0.3-0.5 and 1.9-2.0 in *Procetichthys*; 0.2-0.3 and 1.3 in *Gyrinomimus andriashevi*; 0.6 and 0.1 in *Cetostoma regani*), coupled with the range of sizes of *C. regani* with larger eggs (120-246 mm), suggest that the multiple spawnings do not occur in the same spawning season, but are spread over more than one year. It it also possible that the smaller eggs are resorbed upon full maturation. More data are required to comment on seasonality. Two of the three specimens detailed above were taken in southern temperate waters in March (autumn), while the *C. regani* was taken in northern temperate waters at the end of May (spring), with the few remaining 0.6 mm eggs suggesting an earlier spawning. It appears that different taxa have different size eggs at spawning, with *Procetichthys* having at least 2.0 mm eggs, *Gyrinomimus* at least 1.3 mm and *Cetostoma* and perhaps *Ditropichthys* in the 0.5 to 0.6 mm range.

With both males and juveniles/larvae under 25 mm unknown, discussion of reproductive strategies is speculative. However at least some evidence indicates spawning occurs at bathypelagic depths rather than near the surface. All species have ovaries that increase in size with age and usually larger egg sizes are restricted to the largest individuals (see Figs 14, 22); apparently the largest individuals are those most likely to spawn. For those species with a reasonable sample size, it is clear that the largest individuals are the deepest dwelling (Figs 16, 24). Although there may be limited vertical migration of *Cetostoma regani* to 300 m, no individual larger than 160 mm has been taken in waters shallower than 1000 m (Fig. 24). Although a few smaller individual have eggs larger than 0.1 mm, the majority with larger eggs exceed 160 mm, suggesting spawning takes place below 1000 m (admittedly a spawning migration to shallower waters would presumably be brief and likely to be missed). Possibly the fertilised eggs ascend to the epipelagic waters where planktonic food is more abundant, as is the case for the bathypelagic ceratioid anglerfishes, where the larvae are well known from the upper 300 m (Bertelsen, 1951). As the largest ovaries have thousands of eggs (e.g. *Procetichthys kreffti*), and there may be as many as 2800 cetomimids per cubic kilometre of seawater in the richest areas, the lack of identified cetomimid larvae in the numerous plankton tows taken throughout the world is disconcerting. Presumably the larvae are either so unlike the adults they have not been identified or are so fragile they are damaged beyond recognition in the net. However the larva from a 2 mm egg should be relatively robust. Cetomimid larvae may live in the meso- or bathypelagic, and have smaller opportunity to be sampled. There is no indication of internal fertilisation and direct development, the final possibility which would seem to be precluded by the large number of ovarian eggs.

The final mystery concerns the whereabouts of the male whalefishes. A number of possibilities exist. Although gonads of eight specimens have been sectioned and all found to be females, the smallest specimens were a 133 mm *Cetostoma regani* and a 59 mm *Ditropichthys storeri*. It is possible that the species are sequential hermaphrodites and the small males have not been sampled. Another possibility is that cetomimids are so sexually dimorphic that the males are currently placed in another taxon. Gosline's (1971) suggestion that megalomycterids are macrosomatic male cetomimids is thus appealing, but is not supported by the available evidence (one holotype was described as a female, and the finray counts of only one of the four megalomycterid genera match any of the nine cetomimid genera).

Looking at other possible taxa, one finds the statement of Robins (1974), also without elaboration, that some of the mirapinniform fishes are prejuveniles of cetomimids. Bertelsen & Marshall (1984:382) have summarised the differences between the mirapinnatoids and cetomimoids, which include presence versus absence of pelvic fins, jaw size and shape and principal caudal fin ray counts. The largest *Eutaeniophorus* and *Parataeniophorus* specimens known are 53 and 46 mm long respectively (Bertelsen & Marshall, 1984), considerably overlapping the smallest known cetomimid (*Ditropichthys*) at 25 mm. Mirapinnids are certainly not prejuvenile cetomimids and with at least the holotype and only specimen of *Mirapinna essau* identified as a 39 mm juvenile female (Bertelsen & Marshall, 1984), the family is an unlikely candidate for the missing cetomimid males. Other possibilities are that the sex ratio is skewed with few males, or that the males (and gravid females?) live deeper and have not yet been collected.

If male cetomimids are macrosomatic, as is the case with many other bathypelagic families, the possibility exists that the cavernous tissue of females may be involved with the attraction of males, perhaps in pheromone production. Perhaps the anal lappets, associated at least anteriorly with cavernous tissue in all taxa with lappets except *Rhamphocetichthys* (which lacks cavernous tissue), function in some kind of fanning or primitive pumping mechanism, although no distinctive muscles are apparent.

Distribution

Horizontal. A discussion of distribution patterns is severely limited by the small sample size, with six of the eight species considered in this paper represented by fewer than ten captures (Figs 11, 15, 23). Nonetheless a few generalisations are possible, particularly with consideration of 13 species distributions of the genus *Gyrinomimus* (Paxton, ms) and more than 100 captures of *Cetomimus* not identified to species.

The family Cetomimidae is found in all major oceans, from 52°N to 72°S. Whalefishes occur in the Gulf of Mexico and at least the southern portions of the Gulf of California and Okhotsk Sea, but not in the Mediterranean Sea or Bering Sea. The two commonest species, *Cetostoma regani* and *Ditropichthys storeri*, have cosmopolitan distributions between 50°N and 40°S. The Atlantic distribution of *D. storeri* is similar to the tropical-subtropical pattern found for mesopelagic myctophids (Backus *et al.*, 1977:fig. 2), with only one northern capture clearly beyond the boundaries of the region. *C. regani* on the other hand, with a number of captures in the north Atlantic temperate region, clearly has a more extensive distribution than any of the mesopelagic patterns described. While occurring in all three oceans, *Danacetichthys galathenus* has a narrower latitudinal range from 30°N to 22°S, but is only known from six specimens. A similar cosmopolitan distribution with latitudinal range from 29°N to 5°S is displayed by eight specimens of *Gyrinomimus bruuni*, while 12 specimens of the closely related *Gyrinomimus* sp. C range from 52°N to 26°S in two oceans. The seven captures of *Cetichthys parini* are restricted to the central and the north Pacific and tropical east Indian Oceans. Of the two most frequently captured species of *Gyrinomimus*, 23 specimens of *Gyrinomimus* sp. H are restricted to the north Pacific between 39°N and 52°N, while 24 specimens of *G. grahami* have been taken circumglobally in the Southern Ocean south of the Subtropical Convergence between 32°S and 72°S. Although *G. andriashevi* and *Notocetichthys trunovi* have only been taken twice in southern latitudes, each may eventually display similar distribution patterns.

Thus two general patterns of distribution are apparent for whalefishes. The cosmopolitan pattern, which may prove to be the most common for cetomimids, is typical of other bathypelagic species, such as five species of gigantactinid anglerfishes (Bertelsen *et al.*, 1981:figs 64-69) and at least six species of linophrynid anglerfishes (Bertelsen, 1982:table 3). These cosmopolitan species cross numerous water mass boundaries, unlike most mesopelagic species (see Backus *et al.*, 1977). With water masses best developed in the upper 1000 m (Sverdrup *et al.*, 1942:fig. 209B), the deeper dwelling bathypelagic species have weaker boundaries with which to contend. Nevertheless some cetomimids, such as the north Pacific boreal species of *Gyrinomimus* and the subantarctic species, are clearly restricted to areas of one or a few water masses, as are most of the anglerfishes of the genus *Oneirodes* (Pietsch, 1974:91). Bertelsen *et al.* (1981:72) suggested the difference in shape between the more globose *Oneirodes* and the more hydrodynamic *Gigantactis* in part accounted for the different distribution patterns, with the latter actively moving between water masses. Such shape differences are not apparent between the two localised species of *Gyrinomimus* and the other cetomimids, and some other factor must be of more importance.

The species of *Oneirodes* are not found in the unproductive areas of the central water masses (Pietsch, 1974), whereas the gigantactinids show no such restrictions (Bertelsen *et al.*, 1981:68). The majority of cetomimid specimens have been taken relatively close to land masses or islands, particularly in the north Atlantic and Pacific, in the areas of greatest sampling effort. The apparent absence of *Cetostoma* and *Ditropichthys* in the central areas of the north and south Atlantic (Figs 15, 23) clearly reflects the lack of deep trawling in those areas (Fig. 30). Cetomimids appear similar to gigantactinids in having broad geographic distributions that include central water masses.

The presence of two different patterns of distribution within the family Cetomimidae is not surprising, as other bathypelagic fish families show a range of distribution patterns, from the species of *Oneirodes* restricted to one water mass (Pietsch, 1974), to the species of *Saccopharynx* restricted to one ocean (Nielsen & Bertelsen, 1985:202) to the cosmopolitan species of *Gigantactis* (Bertelsen *et al.*, 1981). As with fishes of other oceanic zones, bathypelagic fishes display a range of distribution patterns from restricted to cosmopolitan. When more sampling effort is put into the vast bathypelagic area, and distribution patterns become clearer, a higher proportion of wide ranging species may be found in bathypelagic waters due to the relative weakness of boundaries in deeper waters and the

more widespread water masses at those depths.

Vertical. The problem of ascertaining vertical distributions from open net captures has been highlighted in many studies. One is forced to use the deepest point the net reached, which is usually the level at which the net spent the most time, and assume the specimens had the best chances of being caught at that depth, even though the net was open and fishing at shallower depths. To complicate matters the fishing depths of the deepest trawls are often an approximation, as they are beyond the range of depth recorders. It is these approximate deepest possible capture depths which have been plotted for the vertical distributions (Figs 12, 16, 24). Fortunately 28 of the 259 specimens reported here were taken in closing nets, providing for three of the eight species some confirmation of living depths.

All cetomimids studied to date are bathypelagic in habitat, with captures below 1000 m. Two species, *Ditropichthys storeri* and *Cetostoma regani*, also live in mesopelagic waters between 600 to 1000 m, at least as juveniles and small adults. The latter species occasionally (4% of specimens) extends into the upper 500 m with one specimen taken at 110 m. There is a strong indication of vertical migration for the smaller specimens of both species. All of the six specimens of *D. storeri* taken above 1000 m were taken in night hauls, during a trawl which included both day and night hours or where time data were not available, as were 15 of the 16 specimens of *C. regani* trawled at 700 m or above. The nocturnal closing net captures below 1000 m clearly show that not all specimens vertically migrate and the small numbers indicate migration is an unusual phenomenon. Both species show a trend for larger individuals to inhabit deeper water, confirmed at least for *C. regani* with a 1500 to 1600 m closing net capture of a 200+ mm individual. It is not clear whether the large number of both species taken in the 2000 to 2200 m range reflects actual living depths or the large number of trawls taken at those depths, particularly by ISH. The vast majority of closing net trawls taken on the RV *Discovery* by IOS were taken above 1500 m, although more than 150 fished to below 1500 m (Merrett, *in litt.*, Aug. 1988) and caught few cetomimids. Nevertheless, as both species have vertical ranges that extend above the bathypelagic zone, the two species with the broadest vertical range also have the widest horizontal distribution; none of the 13 species of *Gyrinomimus* studied have as wide a geographic distribution as *Ditropichthys* or *Cetostoma*.

The other six species detailed in this paper are represented by only 25 specimens. All but the species of *Cetichthys* have been taken in trawls fishing from 1000 to 2300 m deep. The four closing net captures of *C. parini* between 2700 and 3200 m confirm this genus as the deepest dwelling of all cetomimids. Grey (1957:311-312) listed 17 species of bathypelagic fishes found below a depth of 2000 m. *C. parini* is the only cetomimid that can unequivocally be added to this list due to closing net captures. However *C. indagator* and *Procetichthys kreffti* have only been taken in open nets fishing below 2000 m, and can provisionally be added.

The vast majority of whalefishes have been taken in midwater trawls fishing well off the bottom. However, the holotype of *Gyrinomimus grahami* was taken in a bottom trap at 2400 m and the two type specimens of *Notocetichthys trunovi* were taken in two separate trawls within 100 m of the bottom at 1200 to 1400 m. Some cetomimids may be benthopelagic some of the time.

Abundance. Due to the previous paucity of specimens, whalefishes have always been considered very rare. The accumulation of more than 500 specimens requires a reanalysis of this idea. With a centre of distribution below 1000 m (Fig. 12), many species are clearly below the sampling levels of most midwater fish surveys. For instance the Atlantic mesopelagic survey of Backus *et al.* (1977) utilised 1022 midwater trawls, but only 69 of 2254 trawling hours were spent below 1000 m.

One of the most extensive collections of bathypelagic fishes is that of the Institut für Seefischerei in Hamburg (ISH), collected in the Atlantic and Antarctic by the fisheries research vessels *Walther Herwig* and *Anton Dohrn* between 1966 and 1986. A large commercial herring trawl with a circumference of 1600 meshes (MT 1600) was utilised for most catches (Krefft, 1974; Post, 1987). This trawl has head and foot ropes of 70 to 80 m with a potential mouth area of 20 x 30 m or 600 m^2 (Stehmann, *in litt.*, Oct. 1986; Post, 1987). Although Post (1970: 165) used ca. 700 m^2 as the mouth opening, and Post (1987) 600 m^2, both Gjosaeter & Kawaguchi (1980:28) and Hulley (1986:229) used 300 m^2 in their calculations of mesopelagic fish abundances. Hulley (*in litt.*, 3 Feb. 1988) argues that the effective mouth opening at 3.5 knots must be much closer to 300 than 600 m^2, and 300 m^2 is utilised in the calculations below. Other trawls with 1000 meshes and 1216 meshes have been used less frequently by ISH. Krefft (1974), Tesch (1982) and Post (1987) have summarised data for these collections.

The ISH collections include 170 cetomimids taken in 60 trawls. Of these, 145 specimens or 85% were taken in 49 trawls that fished to a maximum of 1800 to 2600 m. To give a better appreciation of whalefish abundance and distribution, the 89 ISH trawls fished at least to 1800 m are mapped and the 49 trawls positive for cetomimids indicated (Fig. 30). The most striking feature is the 1971 cruise between Buenos Aires and Hamburg, where at least one cetomimid was taken in every trawl fished to 1800 m or below. Other cruises were not as successful, with later cruises in 1979 and 1982 having a combined positive trawl rate of only 25% for the 36 trawls fished at least to 1800 m. Nonetheless the total positive capture rate of 55% for the 89 deep trawls clearly shows that cetomimids are not rare at those depths.

Some of the individual catches are even more surprising. One subantarctic trawl to 2600 m at 54°S captured eight specimens of *Gyrinomimus grahami*; the ovaries were not running ripe and some type of spawning aggregation is not indicated. Four to six specimens of *Cetostoma regani* were taken in four different ISH trawls. Between four and six different species of cetomimids were taken in the same ISH trawl on seven of the 19 deep trawls of the 1971 cruise (no other cruise took more than two

species per trawl and then only once). The number of cetomimid specimens per trawl ranged from one to eleven specimens, with the 1971 deep trawls averaging 5.2 specimens per trawl. While the south Atlantic appears to be richer in whalefishes than the north Atlantic (with a phenomenal 91% positive deep trawls between 0°-40°S), it seems that cetomimids may be one of the commonest bathypelagic fish families below 1800 m in all areas.

Parin (1985) has estimated that some 200 species representing 27 families live in the bathypelagic and abyssopelagic zones. Of these the ceratioid anglerfish families Oneirodidae and Linophrynidae with about 50 and 25 species respectively, are the largest bathypelagic families (although other families, such as the Myctophidae, are larger, very few species are bathypelagic). With an estimated 35 species, the Cetomimidae appears to have the second largest number of bathypelagic species.

Not enough work with large closing nets has been done at these depths to determine relative abundances. However if one assumes the vast majority of whalefishes live at or below 1800 m (in the 1971 *Walther Herwig* cruise 99 cetomimids were taken in 19 trawls below 1700 m and seven specimens taken in 58 trawls from 50-1600 m), some approximation of abundance can be reached by calculating the amount of water filtered when the trawl is at depth. The calculation, 300 m^2 mouth opening x 6160 m (3.5 knots for one hour at depth, Krefft, 1974:228) divided by 5.2 (the average number of specimens per deep trawl) gives one whalefish every 355,000 m^3 of water between 1800 to 2300 m in the south Atlantic, where the richest tows have been made. While this figure indicates approximately 70 m between individuals, a total abundance of more than 2800 whalefishes per cubic kilometre of seawater, at least between 1800 and 2500 m in the south Atlantic, is a much higher number than previously appreciated.

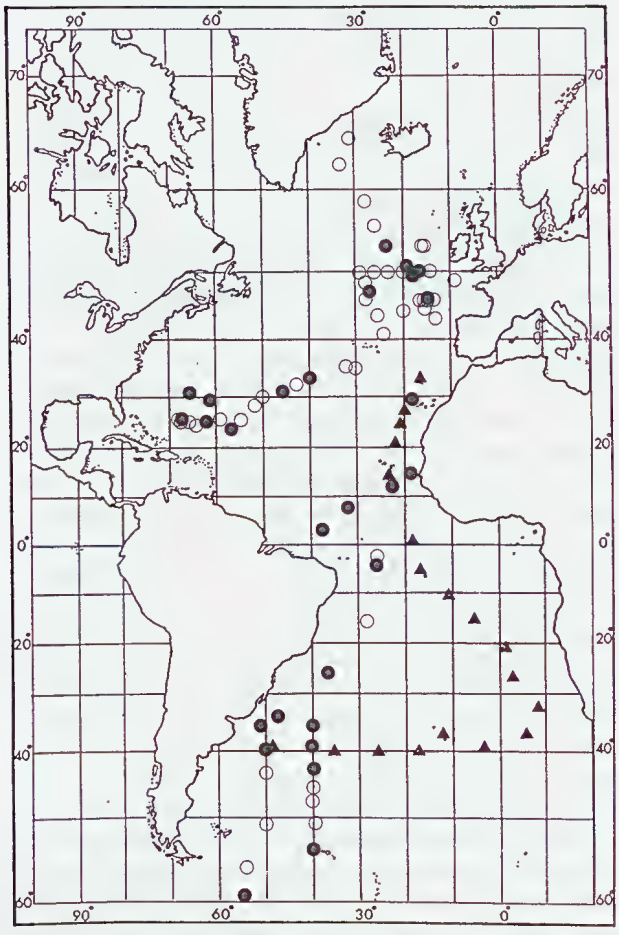

Fig.30. ISH commercial midwater trawls 1968--1986 fished to below 1750 m; solid symbols represent trawls positive for cetomimids; triangles represent one 1971 cruise.

The most abundant whalefishes are clearly *Cetostoma regani* and *Ditropichthys storeri*, with 141 and 77 specimens collected respectively. No other species of cetomimid is nearly that common; the next most commonly collected are two temperate/polar species of *Gyrinomimus* with 20 to 25 specimens each. The abundance of *C. regani* and *D. storeri* is not solely related to their occurrence in the mesopelagic zone, and therefore easier capture, for more than 100 and 70 specimens respectively have been taken by trawls fishing to 1000 m or deeper. In terms of population size and breadth of distribution, these two highly divergent and unrelated species of whalefishes are by far the most successful of the family.

With six of the eight species considered in this paper represented by less than ten specimens, and four by less than five specimens, it seems probable that additional species of whalefishes exist and have not been captured.

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APPENDIX

Table 3. *Ditropichthys storeri* material examined; * specimens included in counts and measurements Table 4; ** specimens cleared and stained.

	Inst.	Reg.No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
1.	ISH	1083/71(1)	131	39°19'S	03°15'W	SAtl	0-ca.2000	N	19/3/71
2.	ISH	1575/71	128.5*	27°14'S	02°56'E	SAtl	0-2000	N	1/4/71
3.	USNM	200526	124	12°09'S	58°35'E	Ind	0-1600	D	26/8/64
4.	MCZ	43331	123	15°57'S	64°46'E	Ind	0-2407	D	5/6/64
5.	ISH	743/71(1)	116.5*	40°18'S	35°07'W	SAtl	0-1850	N	9/3/71
6.	ISH	607/74	112	07°55'N	32°41'W	NAtl	0-ca.2000	N	21/7/74
7.	AMS	I27264-001	112**	36°49'S	12°17'W	SAtl	0-2000	N	17/3/71
8.	ISH	531/76	109	42°58'S	39°53'W	SAtl	0-2350	D	7/1/76
9.	ISH	1083/71(2)	107						
10.	SIO	53-340	104	41°12'N	168°17'E	NPac			10/9/53
11.	ZIN	47882	104			NPac	0-5000		23/5/53
12.	TH	831588	102.5	23°03'N	150°17'E	NPac	0-1577	D	2/6/83
13.	ISH	773/79	101.5	25°31'N	62°00'W	NAtl	0-1800	ND	6/4/79
14.	LACM	44682-1	94.5			NPac			12/11/79
15.	ISH	3446/71	94	39°55'S	26°02'W	SAtl	0-ca.2000	N	11/3/71
16.	OSUO	2513	91.8	39°46'N	128°00'W	NPac	0-2315	N	11/12/81
17.	ISH	2897/71(1)	88.5*	20°27'N	21°58'W	NAtl	0-2100	N	18/4/71
18.	LACM	30599-1	87.8*	33°22'N	118°02'W	NPac	0-1300	N	12/9/68
19.	SIO	64-39	86.0	28°32'N	118°17'W	NPac	0-1800	ND	11/2/64
20.	TH	790081	86	30°16'N	144°35'E	NPac	1329-1541cl	N	11/6/79
21.	AMS	I18816-001	84.4*	33°22'N	118°02'W	NPac	0-1800	D	11/10/68
22.	AMS	I21143-001	84	21°25'N	158°25'W	NPac			1/16/76
23.	AMS	I18821-001	83**	31°40'N	118°39'W	NPac	0-1400	N	4/2/69
24.	ISH	364/79	81.3*	23°46'N	58°59'W	NAtl	0-1200	D	28/3/79
25.	ISH	127/76(1)	81.0*	40°20'S	50°02'W	SAtl	0-2350	D	19/11/75
26.	ISH	127/76(2)	81						
27.	SIO	64-24	80.5	23°54'N	113°39'W	NPac			4/2/64
28.	ZIN	47878	80.3*	45°16'N	156°13'E	NPac	0-5000		23/1/53
29.	ISH	2950/71	79	23°47'N	20°59'W	NAtl	0-2100	N	19/4/71
30.	ZIN	47881	79.0*	19°50'N	68°14'W	NAtl	0-2000		3/2/73
31.	ISH	905/79(1)	75.2*	24°41'N	66°20'W	NAtl	0-1800	N	18/4/71
32.	ISH	2897/71(2)	75.0*						
33.	ISH	743/71(2)	74.6*						
34.	LACM	44681-1	71.5			NPac	0-1000		24/10/74
35.	ISH	743/71(3)	69.0*						
36.	ISH	1580/68	66.9	34°01'S	47°39'W	SAtl	0-2000		15/2/68
37.	LACM	9730-30	65**	30°50'N	118°39'W	NPac	0-ca.1300	D	5/1/66
38.	SIO	78-189	62.3	30°57'N	120°46'W	NPac	0-1800	N	13/8/75
39.	ISH	905/79(2)	60.0*						
40.	ISH	743/71(4)	59.0*						
41.	MCZ	50691	58	23°02'N	45°33'W	NAtl	0-1100	N	17/10/73
42.	ISH	127/76(3)	57						
43.	ZMUC	P2340007	56.9*	14°37'N	119°52'E	NPac	0-ca.800		17/6/29
44.	ZMUC	P2340008	55.5*	00°31'S	11°02'W	SAtl	0-ca.2000		4/3/30
45.	LACM	9661-8	55.2	27°18'N	115°19'W	NPac	0-ca.1200	D	16/6/67
46.	LACM	44391-1	55.1	27°48'N	88°45'W	NAtl	0-ca.2000		30/7/59
47.	ISH	995/71	54.3*	36°49'S	12°17'W	SAtl	0-2000	N	17/3/71
48.	LACM	8988-33	54.0	28°54'N	118°10'W	NPac	0-?1200	N	6/5/65
49.	AMS	I18826-001	53.3*	21°25'N	158°25'W	NPac	0-1200	D	9/12/73
50.	LACM	9350-28	51.6	29°30'N	118°25'W	NPac	0-ca.1200	ND	28/8/65
51.	SIO	63-540	50.8	32°27'S	08°49'E	SAtl	0-3400	DN	6/6/63
52.	SIO	60-232	50	04°59'S	135°19'W	SPac	0-2750		1/7/60
53.	TH	800405	49	30°34'N	147°31'E	NPac	0-3156	ND	3/6/80
54.	MCZ	43337	49	07°55'N	64°55'E	Ind	0-2850	D	23/5/64

	Inst.	Reg.No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
55.	IOS	5809	48.1*	28°06'N	14°05'W	NAtl	0-800	N	6/11/65
56.	ZMUC	P2340006	48.0*	30°08'S	176°50'W	SPac	0-ca.1650	D	14/12/28
57.	SIO	78-61	46.6	21°25'N	158°25'W	NPac	900-1100cl	D	24/5/71
58.	LACM	30179-9	46.5			NPac			28/5/68
59.	ISH	2296/71	44.7*	01°04'N	18°22'W	NAtl	0-2100	N	12/4/71
60.	CAS(SU)	63730	43	32°12'N	64°36'W	NAtl			13/9/30
61.	MCZ	50690	43	33°50'S	87°41'W	SPac	0-2900	ND	17/1/66
62.	SIO	70-327	41.5	18°20'N	133°29'E	NPac	0-1500	N	9/8/70
63.	MCZ	60394	41			NAtl			
64.	IOS	3661	40.2*	41°N	19°W	NAtl	0-1500		14/3/58
65.	ZIN	47879	40.1*	11°55'S	84°11'E	Ind			
66.	ZIN	47880	40	04°50'S	23°27'W	SAtl	0-1100		13/1/72
67.	SIO	63-425	38.2	27°46'N	129°15'W	NPac	0-1500	D	2/4/62
68.	SIO	70-332	37.4	18°14'N	127°16'E	NPac	0-1700	D	12/8/70
69.	MCZ	43338	36	19°24'S	65°30'E	Ind	0-2600	D	8/6/64
70.	SIO	70-336	35.1	18°50'N	124°10'E	NPac	0-1525	D	19/8/70
71.	SIO	70-112	35.1	24°39'S	155°00'W	SPac	0-1150	N	3/10/69
72.	AMS	I21144-001	34	21°25'N	158°25'W	NPac			2/5/78
73.	IOS	11261	34	31°32'N	25°26'W	NAtl	1200-1300cl	N	7/7/85
74.	UMML	14840	34	23°39'N	82°45'W	NAtl	0-777		20/1/64
75.	LACM	32747-1	33.4	21°25'N	158°25'W	NPac	0-1000	D	16/12/70
76.	LACM	32740-6	32.9	21°25'N	158°25'W	NPac	0-1150	D	21/9/70
77.	SIO	68-490	32.7	28°57'N	178°09'E	NPac			22/9/68
78.	LACM	32749-6	30.0	21°25'N	158°25'W	NPac	0-1000	D	1/3/71
79.	IOS	10380	29.5	29°54'N	34°15'W	NAtl	1400-1500cl	D	18/6/81
80.	UMML	9724	29	15°00'N	67°05'W	NAtl	0-877		17/11/60
81.	USNM	200527	28.7	01°50'N	65°06'E	Ind	0-1250	N	27/5/64
82.	ISH	1330/79	27.6*	31°11'N	63°27'W	NAtl	0-ca.1700	D	19/4/79
83.	MCZ	60738	26.8*	03°39'N	41°38'W	NAtl	0-ca.650	N	16/7/83
84.	BOC	2134	25	22°43'N	74°23'W	NAtl	0-ca.800		29/3/27

Table 4. Morphometrics of 26 specimens of *Ditropichthys storeri* as % SL: average (minimum-maximum) standard deviation.

SL	26.8-27.6	40.1-60.0	69.0-88.5	116.5-128.5	26.8-128.5	
n	2	11	11	2	26	
HL	29.7(29.1-30.2)0.78	31.7(29.7-33.9)1.35	32.6(30.9-34.9)1.50	31.3(31.0-31.6)0.42	31.8(29.1-34.9)1.44	(n=23)
SnL	9.5(9.4-9.7)0.21	11.6(9.7-14.4)1.25	11.3(9.9-12.8)0.85	11.7(11.2-12.2)0.71	11.3(9.4-14.4)1.11	
PmL	19.9(19.2-20.5)0.92	21.0(19.3-23.4)1.28	21.2(19.7-22.6)0.96	21.3(20.6-21.9)0.92	21.0(19.2-23.4)1.11	
LJL	20.6(19.8-21.4)1.13	22.0(20.7-232)0.99	21.9(20.8-23.3)0.82	20.6(20.3-20.9)0.42	21.7(19.8-23.3)0.99	(n=25)
Pm-Op	13.4(n=l)	12.0(10.2-13.0)1.25	13.0(10.1-16.4)1.75	12.5(12.4-12.5)0.07	12.5(10.1-16.4)1.48	(n=25)
ED	1.9(1.8-1.9)0.07	1.7(1.4-2.2)0.27	1.3(1.1-1.5)0.13	1.1(1.0-1.1)0.07	1.5(1.0-2.2)0.34	
EW		10.9(8.7-12.6)1.43	11.5(10.2-12.1)0.71	13.4(12.8-14.0)0.85	11.4(8.7-14.0)1.35	(n=20)
HW	8.8(8.2-9.4)0.85	15.4(13.3-17.3)1.29	15.7(13.8-17.3)1.02	15.5(14.8-16.2)0.99	14.9(8.2-17.3)2.21	(n=23)
PmW		12.8(11.4-14.8)1.22	13.9(12.3-16.6)1.68	13.8(12.9-14.7)1.27	13.3(11.4-16.6)1.42	(n=20)
BD	20.5(17.2-23.9)4.74	22.8(20.7-24.4)1.19	25.0(20.2-27.9)2.09	26.9(25.4-28.4)2.12	23.9(17.2-28.4)2.47	
D-A	12.7(11.9-13.4)1.06	15.7(12.0-18.3)1.78	16.7(14.2-19.2)1.38	19.1(n=1)	16.1(11.9-19.2)1.99	(n=25)
CPD	4.6(4.1-5.1)0.71	6.0(4.7-7.0)0.67	6.4(5.5-7.5)0.61	6.7(6.7-6.8)0.07	6.1(4.1-7.5)0.78	
CPL	13.4(12.3-14.5)1.56	15.7(13.5-18.3)1.27	15.1(13.6-16.2)0.76	15.5(15.2-15.9)0.49	15.3(12.3-18.3)1.17	
Sn-P	33.1(29.5-36.6)5.02	34.5(32.0-37.8)1.72	35.2(33.5-37.0)1.39	32.7(32.6-32.9)0.21	34.5(29.5-37.0)1.94	(n=25)
PL	10.1(8.6-11.6)2.12	11.3(9.2-15.0)1.92	10.8(9.7-12.6)0.90	9.1(8.2-10.0)1.27	10.5(8.2-15.0)1.15	(n=18)
Sn-D	64.9 (n=1)	64.7(63.2-66.6)1.15	66.1(64.6-68.7)1.26	65.0(64.0-66.0)1.41	65.2(63.2-68.7)1.27	(n=23)
DB	24.3(23.6-25.0)0.99	23.6(22.0-26.6)1.32	24.0(20.9-26.1)1.33	24.6(23.4-25.8)1.70	23.9(20.9-26.6)1.28	
Sn-A	62.7 (n=1)	67.1(62.4-70.7)2.28	68.0(66.5-69.2)0.98	68.3(67.3-69.3)1.41	67.4(62.4-70.7)2.01	(n=23)
AB	16.5(16.4-16.7)0.21	16.8(15.1-19.8)1.35	17.1(15.9-19.1)1.02	16.3(15.8-16.9)0.78	16.9(15.1-19.8)1.11	
An-AO	1.7(1.5-1.8)0.21	1.8(1.0-2.7)0.49	2.3(1.0-3.7)0.85	3.5(2.7-4.3)1.13	2.1(1.0-4.3)0.81	
D	20(20)0	20.2(19-22)0.98	20.4(19-22)0.86	20(19-21)1.41	20.3(19-22)0.88	
A	17(n=1)	17.1(16-18)0.83	17.0(16-18)0.45	16.0(15-17)1.41	17.0(15-18)0.73	(n=25)
P		19.1(18-21)0.99	19.1(18-21)0.86	17.5(17.18)0.58	18.9(17-21)1.03	(n=24)
Vert	39 (n=1)	39.7(39-41)0.75	39.6(38-41)0.88	40(39-41)1.0	39.7(38-41)0.84	(n=25)
LLSc	12(n=1)	11.9(11-13)0.57	11.2(10-13)0.92	13(n=1)	11.8(10-13)0.80	(n=22)

Table 5. Morphometrics, as % SL, and meristics of specimens of *Cetichthys*. * indicates holotype; ** indicates damage or distortion; LJT = lower jaw teeth.

	Cetichthys indagator				*Cetichthys parini*							
Inst.	ISH	ZMUC	LACM	NSMT	SIO	OSU	SIO	OSU	ZIN	AMS	NSMT	ZIN
Reg. No.	1186/71	P23451*	11314-1	P44368	53-344*	2552	87-9	2553	47877	I.27258-001	P60001	47876
SL	128.8	117.7	92.5	51.5	196.2	174	157.2	121.6	104.2	96.0	88.6	87.5
HL	31.2	31.9	33.5	**	33.4	31.6	32.3	32.1	38.4	36.7	36.1	38.5
SnL	11.3	11.0	11.4	11.5	12.3	**	10.9	12.0	13.0	12.7	13.4	14.3
PmL	22.9	22.9	26.5	**	23.5	22.7	24.3	25.9	28.2	26.3	28.1	29.4
LJL	21.4	22.9	27.2	26.4**	22.8	20.7	25.2	24.8	29.1	25.6	28.2	29.6
Pm-Op	9.1	10.3	7.5	**	10.4	10.1	8.4	7.5	10.2	8.6	7.6	9.1
ED	1.3	1.3	1.1	1.9	0.7	**	0.8	0.9	1.2	1.3	1.0	1.1
EW	**	10.6	8.6	**	12.8	**	10.1	12.7	11.1	9.4	10.5	7.4
HW	14.9**	16.0	18.1	12.8**	19.0	18.7	13.4	17.8	19.8	16.1	17.0	16.8
PmW	10.6	9.4	14.3	**	16.3	16.6	9.5	14.1	15.5	10.8	12.6	12.2
BD	**	22.6	22.0	14.6	25.0	22.4	20.1	21.4	22.0	20.3	20.1	21.0
D-A	**	24.0	21.6	15.9	20.6	17.5	15.9	16.4	19.2	18.2	12.9	17.7
CPD	8.5	8.3	9.0	6.2	7.9	7.6	6.9	7.0	7.2	6.4	5.0	6.2
CPL	24.5	24.1	24.1	24.7	16.7	19.1	17.3	19.1	19.2	18.8	18.1	19.2
Sn-P	**	35.3	36.8	32.8	35.6	33.0	34.3	33.2	38.9	36.9	36.9	40.3
PL	**	8.8	10.6	7.0	6.5	5.5	6.2	5.2	7.9	**	9.0	8.6
Sn-D	63.3	70.3	65.1	61.0	69.6	67.5	68.6	66.0	74.0	68.2	68.5	69.7
DB	13.0	11.7	14.8	17.1	15.6	13.9	14.6	14.2	13.9	14.3	14.4	16.3
Sn-A	**	72.4	69.7	61.6	70.3	71.6	69.3	71.5	72.0	69.2	66.5	67.5
AB	9.3**	7.1	7.9	9.9	14.2	11.5	12.7	13.8	13.2	13.2	13.2	14.3
An-AO	**	8.9	8.1	6.2	8.8	7.9	8.3	8.6	8.5	7.0	5.0	7.0
CopL	4.1	4.8	5.6	11.7	3.5	4.4	4.6	6.2	7.4	7.3	8.9	8.8
CopL/W				3.6			6.6			5.9	8.8	
D	14	14	14	15	14	14	16	14	15	13	13	16
A	**	13	12	13	13	12	14	13	14	13	13	14
P	**	21/21	21/?	21/?	?/?	20?/19?	22/22	19/19	23/24	22?/21?	21/21?	23/?
C	12	13	12	**	**	12	11	11	12	12?	12	12?
Vert	25+17=42	25+17=42	25+18=43	25+18=43	24+15=39	26+15=41	25+16=41	25+16=41	24+16=40	25+16=41	24+17=41	24+16=40
LLSc	14?/?	13/13	14/13	13?/?	8/8	9/?	9/9	10?/?	?/?	9/?	?/?	9/?
GRArch1	3+9	3+9/10	3+9	3+10	3+8	3+7	3+9	3+7	3+7/8	3+9	3+8	3+8
GRArch4	1+6	2+7	1/2+7	1+7	2+6	1+5	2+6	1+4/5	1/2+5	1+5	2+5	2+5
LJT		108/112	112		171/178	150		170	113/120	119		95

Table 6. Morphometrics, as % SL, and meristics of specimens of *Notocetichthys*, *Danacetichthys* and *Rhamphocetichthys*. * indicates holotype; ** indicates damage or distortion; Vom T = vomerine teeth.

	Notocetichthys trunovi		*Danacetichthys galathenus*					*Rhamphocetichthys savagei*				
Inst.	ZIN	ZIN	NSMT	USNM	ISH	ZMUC	SIO	ZMUC	MCZ	AMS	LACM	ISH
Reg.No.	47697	47696*	P60002	200525	1944/71	P2340563*	70-327	P2340564	60342*	I.26872-001	30034-11	2297/71
SL	109.0	107.5	53.9	53.5	48.6**	39.3	38.1	34.0	125.7	98.5	90.8	110
HL	31.3	31.9	36.5	36.6	37.4	37.7	37.0	35.3	35.1	34.9	38.3	34.5
SnL	12.5	10.8	12.6	12.1	11.3	12.7	11.3	11.5	16.8	16.2	18.1	17.7
PmL	22.3	21.1	30.2	31.4	29.0	30.8	30.7	29.4	25.8**	28.2	31.3	30.5
LJL	20.6	21.2	29.9	32.1	27.6	31.0	29.9	28.8	24.2**	28.2	34.9	28.2
Pm-Op	8.3	9.8	7.8	9.2	**	10.9	7.8	7.4	8.7	5.5	5.2	3.6**
ED	1.4	1.0	2.2	2.4	2.1	2.0	2.4	2.1	1.4	1.6	1.7	1.4
EW	10.2	7.6	13.9	10.3	**	9.9	12.6	12.6	5.3	5.2	4.7	3.2
HW	12.9	11.4	21.2	16.4	**	14.5	22.0	21.2	8.0	13.2	11.5	7.5
PmW	10.7	13.8	16.7	**	**	6.4**	12.9	11.8	8.8**	7.5	8.0	7.7
BD	18.9	26.0	22.6	17.0	**	17.3	21.9	21.5	12.8	**	13.9	**
D-A	19.8	20.5	13.7	11.4	14.8	12.0	15.5	14.7	10.3	9.9	10.2	10.1**
CPD	8.3	8.4	7.6	8.4	7.6	5.9	8.9	7.6	4.7	3.3	3.4	3.4
CPL	18.2	20.2	10.4	12.5	15.4	9.9	11.5	17.4	11.6	14.7	15.4	13.9
Sn-P	34.8	35.3	36.4	36.6	**	38.7	37.8	35.3	37.0	**	40.2	**
PL	7.7	11.9	13.4	8.2**	**	**	**	9.7	9.7	12.2	8.0	8.7
Sn-D	68.5	69.7	73.3	68.0	**	73.5	73.2	67.6	73.6	71.6	72.4	73.6
DB	11.7	11.7	13.9	12.7	16.9	14.0	13.9	17.4	13.3	10.9	11.3	9.8
Sn-A	74.3	71.0	74.4	70.3	**	77.4	76.4	63.2	75.7	74.7	72.0	74.5
AB	9.9	10.6	12.8	11.6	17.1	12.2	13.1	17.1	12.5	10.3	10.5	9.1
An-AO	9.9	8.1	2.0	1.9	2.1	2.3	2.1	1.2	1.1	2.6	3.3	1.8
CopL	0.9	1.1	10.2	14.6	10.3	15.0	13.9	10.0	8.4	9.6	9.3	8.7
CopL/W	1.1	2.4	5.5	5.6	4.5	4.5	5.9	3.7	5.0	7.3	4.9	4.6
D	13	13	15	15	16?	14	13+?	15	17	15	15	15
A	11	13	14	14	15	15	12+?	14	17	15	15	15
P		19/17	22/21	?/?	22/?	21?/?	21?/?	21?/23	23?/24	21/?	22/23	22/22
C	10	12	14	14?	13	?	?	15?	16	16	17	16
Vert	26+15=41	24+15=39	28+15=43	28+16=44	26+20=46	29?+16=45?	29+15=44	26+19=45	27+16=43	27+17=44	27+17=44	29+16=45
LLSc	16/?	15	18/18	?/?	17?/?	17/17?	?/?	18?/16?	33	32	31/32	40
GRArch1	2+8	2+8	2+7	2+8	2+7	2+7	2+7	2+7	1+7/8	3+7	3+7	0/1+4/5
VomT	0	0	15	42	46	22	19	25	?	?	?	?

Table 7. *Cetostoma regani* material examined; ! holotype; * specimens with dorsal counts included, Fig. 25; ** specimens included in measurements Table 8 and Fig. 25; *** specimens cleared and stained; + plus length of missing head, specimens not included in vertical distribution Fig. 24.

	Inst.	No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
1.	ISH	894/82	246.5**	49°52'N	16°52'W	NAtl	0-3200	D	19/6/82
2.	ISH	1695/71	211.0**	21°35'S	02°00'W	SAtl	0-2100	N	3/4/71
3.	LACM	9571-3	206.8**	31°21'N	120°46'W	NPac	0-ca.1400	N	16/1/66
4.	IOS	10376/38	204.0**	33°21'N	33°35'W	NAtl	1500-1600cl	D	29/5/81
5.	ISH	2896/71(1)	200.0**	20°27'N	21°58'W	NAtl	0-2100	N	18/4/71
6.	ISH	1442/71(1)	199.0**	33°00'S	07°50'E	SAtl	0-2000	N	30/3/71
7.	SIO	51-90	198.2*	25°48'N	114°46'W	NPac	0-2200	ND	21/3/51
8.	ISH	2949/71(1)	196.4**	23°47'N	20°59'W	NAtl	0-2100	N	19/4/71
9.	ISH	609/74	ca.195	07°54'N	32°43'W	NAtl	0-ca.2000	N	21/7/74
10.	IOS	8959(1)	194.1**	28°47'N	15°02'W	NAtl	1000-2000cl	N	31/7/76
11.	ISH	2098/71	188.4**	05°30'S	16°28'W	SAtl	0-1900	N	9/4/71
12.	ISH	626/68(1)	188.0**	12°07'N	23°08'W	NAtl	0-ca.2000	N	30/1/68
13.	ISH	1082/71	185.0**	39°19'S	03°15'W	SAtl	0-ca.2000	N	19/3/71
14.	ISH	1189/71(1)	185*	37°08'S	05°23'E	SAtl	0-2200	N	21/3/71
15.	ISH	2896/71(2)	ca.185						
16.	ISH	3033/71(1)	ca.185*	32°47'N	16°24'W	NAtl	0-1800	N	22/4/71
17.	ISH	1494/79	183.2**	28°41'N	60°54'W	NAtl	0-ca.1800	D	20/4/79
18.	ISH	740/71(1)	182.6*	40°18'S	35°07'W	SAtl	0-1850	N	9/3/71
19.	ZMUC	P2340005	181.0*	23°47'N	20°59'W	NAtl	0-2100	N	19/4/71
20.	ISH	740/71(2)	ca.180*						
21.	ISH	3033/71(2)	ca.180*						
22.	ISH	1189/71(2)	ca.180*						
23.	ISH	740/71(3)	177						
24.	ZIN	47886	175.6	30°51'S	94°47'E	SInd	0-1465		23/9/76
25.	ISH	858/71(1)	ca.175	39°55'S	26°02'W	SAtl	0-ca.2000	N	11/3/71
26.	ISH	2949/71(2)	170.1*						
27.	ISH	2449/79(1)	165.4	35°24'N	31°53'W	NAtl	0-350	N	29/4/79
28.	MCZ	41339	164.4*	28°47'N	87°57'W	NAtl	0-1900		16/7/60
29.	ISH	2449/79(2)	161.3*						
30.	ISH	2991/71	158.0	27°18'N	19°44'W	NAtl	0-2000	N	20/4/71
31.	ISH	589/82	157.5*	47°52'N	27°08'W	NAtl	0-1370	D	13/6/82
32.	HUMZ	78240	157*	40°35'N	142°31'E	NPac	0-1195		13/9/78
33.	ISH	2708/71	ca.152*	14°05'N	23°12'W	NAtl	0-1900	N	16/4/71
34.	ZMUC	P2340000	151*	25°11'N	20°57'W	NAtl	0-ca.2000	D	25/10/21
35.	OSUO	1516	150.0*	44°48'N	138°30'W	NPac	0-2700	ND	25/7/66
36.	ISH	689/76	149*	36°18'S	40°06'W	NAtl	0-2400	D	9/1/76
37.	ISH	858/71(2)	148.5*						
38.	IOS	4711(1)	148*	30°00'N	23°00'W	NAtl	0-1600		3/9/61
39.	OSUO	1515	145.6*	44°38'N	137°38'W	NPac	0-2700	ND	26/7/66
40.	ISH	376/82	ca.144*	43°22'N	25°59'W	NAtl	0-1230	D	9/6/82
41.	ISH	2325/79	140.7*	34°20'N	35°24'W	NAtl	0-170	N	28/4/79
42.	ISH	2896/71(3)	138.3*						
43.	ISH	1442/71(2)	137.4*						
44.	SIO	64-535	136.6			EPac			
45.	ISH	2162/79(1)	134.3	32°59'N	39°41'W	NAtl	0-1950	D	27/4/79
46.	IOS	10380/5	134.0*	30°04'N	33°56'W	NAtl	1100-1200cl	D	17/6/81
47.	ISH	3033/71(3)	133.4*						
48.	ISH	626/68(2)	131.4*						
49.	OSUO	1995	131*	44°32'N	132°12'W	NPac	0-3724	D	1/6/70
50.	ISH	2949/71(3)	130.0*						
51.	BOC	2132	130*	24°11'N	75°37'W	NAtl	0-ca.1500		22/3/27
52.	SIO	78-56	129.7	21°25'N	158°25'W	NPac	0-1100	D	30/8/73
53.	LACM	36047-5	125.5*	05°03'S	129°41'E	SPac	0-960	N	1/5/75
54.	ISH	626/68(3)	124.9						
55.	IOS	8607(1)	124.6**	09°03'N	23°08'W	NAtl	700-800cl	D	22/8/74
56.	IOS	6662/34(1)	124.0*	10°49'N	19°57'W	NAtl	900-1040cl	D	20/2/68

	Inst.	No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
57.	ZIN	47883	ca.122	05°29'N	153°57'E	NPac	0-1000		26/2/75
58.	ZIN	47885	ca.121*	03°08'N	08°54'E	NAtl	0-1550		1/1/76
59.	IOS	7824/17	120.8	10°57'N	20°03'W	NAtl	700-800cl	D	8/3/72
60.	ISH	2633/71(1)	120.1	10°52'N	22°09'W	NAtl	0-608	N	15/4/72
61.	OSUO	1996	120.1*	44°25'N	132°13'W	NPac	0-3655	ND	1/6/70
62.	AMS	I18819-001	120***	10°51'N	19°55'W	NAtl	0-700	N	17/2/68
63.	ISH	2633/71(2)	117.0						
64.	MCZ	60396	117.0**	26°44'N	79°23'W	NAtl			7/8/78
65.	IOS	10523/3(1)	117*	05°32'S	00°31'E	SAtl	700-800cl	D	10/5/82
66.	OSUO	2328	116.5*	44°43'N	125°48'W	NPac	1250-1500cl	N	25/5/75
67.	SIO	70-95	116.0	31°37'N	120°19'W	NPac	0-ca.1100		22/3/70
68.	ISH	3102/71	112.0	27°14'S	02°56'W	SAtl	0-2000	N	1/4/71
69.	ISH	519/74	111.4**	14°11'N	18°28'W	NAtl	0-ca.2000	N	18/7/74
70.	USNM	200530	106.7**	03°55'N	60°08'E	NInd	0-2120	D	18/8/63
71.	ISH	626/68(4)	105.9*						
72.	MCZ	42844	104.9*	02°41'N	28°56'W	NAtl	0-ca.1100	N	28/2/63
73.	OSUO	29	104.9*	44°18'N	125°30'W	NPac	0-1250	ND	15/8/61
74.	ISH	954/68	ca.101*	04°43'S	26°39'W	SAtl	0-2000	D	4/2/68
75.	SIO	69-20	100.8**	06°33'N	114°16'E	NPac			24/4/68
76.	ZMUC	P2340004	98.4*	29°11'N	14°14'W	NAtl	0-ca.1666	D	27/3/30
77.	UMML	20001	97*	00°30'N	05°05'E	NAtl	0-850		23/5/65
78.	IOS	8607(2)	96.1**						
79.	UMML	18352	95	23°43'N	81°47'W	NAtl	0-650		21/1/64
80.	ISH	170/68	94.9*	32°34'N	16°53'W	NAtl	0-1000	N	20/1/68
81.	ISH	2295/71	93.5*	01°04'N	18°22'W	NAtl	0-2100	N	12/4/71
82.	MCZ	60395	93.5*	13°40'N	76°40'W	NAtl			8/10/66
83.	ISH	626/68(5)	87.8*						
84.	SIO	69-334	87.7*	14°57'S	106°06'W	SPac	0-1300	N	
85.	ZMUC	P2340565	87.3*	12°02'S	96°43'E	SInd	0-ca.1150	DN	11/10/29
86.	ISH	2633/71(3)	86.5*						
87.	SIO	68-442	86	19°49'N	168°45'W	NPac	0-1250	N	27/8/68
88.	ISH	2633/71(4)	84.9*						
89.	SIO	69/24	84.6	17°04'S	67°08'E	SInd	0-936	D	25/8/68
90.	ZIN	47884	83.5*	15°11'N	74°11'W	NAtl	0-1000		2/3/73
91.	USNM	200531	83.5*	25°52'S	60°00'E	SInd	0-1420	N	5/9/63
92.	UMML	34423	82.2*	26°00'N	86°00'W	NAtl	0-2000		9/5/88
93.	UMML	34423(2)	80.3*						
94.	LACM	44683-1	79.9						1/8/70
95.	ZIN	PLEBEDEV	79.0	08°29'N	52°24'W	NAtl	0-1200		29/2/64
96.	IOS	4711(2)	79*						
97.	LACM	9747-36	78.5**	32°25'N	117°57'W	NPac	0-ca.1400	N	15/4/66
98.	ZMUC	P2340001	77.5	14°37'N	119°52'E	NPac	0-ca.700	N	17/6/29
99.	SIO	68-442	77.4	22°10'N	171°57'E	NPac		D	17/9/68
100.	MOM	HIR.3215	ca.77!	30°45'N	25°47'W	NAtl	0-2000		8/8/12
101.	MCZ	41343	ca.77	28°50'N	88°08'W	NAtl	0-2450		13/7/60
102.	ISH	2633/71(5)	ca.76*						
103.	LACM	32744-1	75.7	21°25'N	158°25'W	NPac	0-110		7/7/70
104.	SIO	78-57	73.2	21°25'N	158°25'W	NPac	0-1100		26/5/74
105.	IOS	10523/12	71.0*	04°53'S	00°25'E	SAtl	895-1000cl	D	12/5/82
106.	LACM	34279-1	69.2	32°25'N	117°53'W	NPac	0-1400	N	21/1/70
107.	IOS	8959(2)	68.7**						
108.	OSUO	28	68.4*	34°36'N	140°32'W	NPac	0-2450		5/3/65
109.	MCZ	43333	68	04°01'S	65°00'E	SInd	0-615	N	30/5/64
110.	USNM	200528	65.5*	10°01'S	64°19'E	SInd	0-2250	N	2/6/64
111.	SIO	78-69	62.6	21°25'N	158°25'W	NPac	0-1500	N	29/9/72
112.	IOS	10150/1(1)	62.5*	26°01'N	20°21'W	NAtl	0-1035	D	8/10/79
113.	ZMUC	P2340002	62.1*	15°22'N	115°20'E	NPac	0-2333	N	20/5/29
114.	ISH	2162/79(2)	62.0*						
115.	ZMUC	P2340003	61.2*	03°41'N	137°53'E	NPac	0-ca.1000	D	12/7/29

	Inst.	No.	SL	Lat.	Long.	Ocean	Depth(m)	Time	Date
116.	IOS	10150/1(2)	60.2*						
117.	SIO	78-63	59.9	21°25'N	158°25'W	NPac	0-ca.700	N	23/5/72
118.	IOS	10150/1(3)	59.2*						
119.	IOS	6662/16	58.8*	11°01'N	19°50'W	NAtl	810-890cl	N	16/2/68
120.	IOS	10150/1(4)	58.3*						
121.	LACM	32749-1	57.8	21°25'N	158°25'W	NPac	0-1000	D	1/3/71
122.	IOS	7803/2	57.1*	18°09'N	25°12'W	NAtl	1015-1250cl	D	19/2/72
123.	MCZ	42843	55.7	00°17'N	27°31'W	NAtl	0-ca.300	N	19/2/63
124.	USNM	200529	55*	01°50'N	65°06'E	NInd	0-1250	N	27/5/64
125.	LACM	32748-1	53.3	21°25'N	158°25'W	NPac	0-900	D	16/12/70
126.	IOS	6662/7	51.7*	11°09'N	19°46'W	NAtl	710-800cl	N	14/2/68
127.	ISH	1862/79	50.8*	30°43'N	46°14'W	NAtl	0-2000	D	25/4/79
128.	BOC	4899	50.5*	37°43'N	12°07'W	NAtl		N	7/9/59
129.	AMS	I18825-001	50.2	21°25'N	158°25'W	NPac	0-ca.1500	D	7/4/70
130.	IOS	10382/6	49.9**	32°37'N	31°44'W	NAtl	900-1000cl	N	21/6/81
131.	ISH	2633/71(6)	49.2*						
132.	IOS	7824/13	48.9**	10°45'N	20°05'W	NAtl	1000-1250cl	N	7/3/72
133.	IOS	10523/13	48.7*	04°55'S	00°22'E	SAtl	995-1100cl	D	12/5/82
134.	SIO	70-347	47.8	14°20'N	119°47'E	NPac	0-1750	DN	19/9/70
135.	IOS	6662/34(2)	47.7**						
136.	IOS	10523/3(2)	47						
137.	UMML	19988	ca.46	02°47'N	08°45'E	NAtl	0-740		16/5/65
138.	BOC	4900	45*	37°33'N	12°57'W	NAtl		D	19/9/59
139.	UMML	20009	ca.45	03°15'N	04°47'E	NAtl	0-1230		25/5/65
140.	IOS	10233/27	44.1*	32°03'N	31°33'W	NAtl	900-1010cl	D	16/9/80
141.	IOS	10523/1	43.4*	05°25'S	00°31'E	SAtl	500-600cl	D	10/5/82
142.	AMS	I18818-001	43.0*	21°25'N	158°25'W	NPac			
143.	CAS	SU65867(1)	ca.42	32°12'N	64°36'W	NAtl			5/7/30
144.	CAS	SU65867(2)	ca.41						
145.	SIO	68-447	40.7	19°11'N	168°44'W	NPac		DN	29/8/68
146.	IOS	11261/15	39.6*	31°14'N	25°19'W	NAtl	900-1000cl	D	28/6/85
147.	ISH	3033/71(4)	133+						
148.	ISH	268/68	125+	29°23'N	18°10'W	NAtl	0-ca.2000	N	22/1/68
149.	ISH	798/73	109+	48°30'N	18°00'W	NAtl	0-2750	D	26/9/73
150.	ISH	1116/79	93+	25°08'N	67°39'W	NAtl	0-1800	D	12/4/79

Table 8. Morphometrics of 22 specimens of *Cetostoma regani*, as % SL: average (minimum-maximum) standard deviation.

SL(mm)	47.7-78.5	96.1-124.6	183.2-246.5	47.7-246.5	
n	5	6	11	22	
HL	29.7(27.4-31.4)1.65	25.4(23.6-26.5)1.07	24.0(22.3-26.0)1.09	25.9(22.3-31.4)2.67	(n=19)
SnL	11.3(8.7-12.5)1.33	9.0(7.9-10.0)0.69	8.4(7.9-9.1)0.39	9.5(7.9-12.5)1.47	(n=17)
PmL	21.2(18.0-23.5)2.01	16.8(15.4-18.6)1.17	17.0(15.4-18.2)0.88	17.9(15.4-23.5)2.24	(n=21)
LJL	22.0(19.2-24.7)1.76	17.8(16.8-19.4)0.97	17.5(15.9-19.3)1.03	18.6(15.9-24.7)2.23	
Pm-Op	8.2(7.6-8.8)0.40	8.1(7.4-8.8)0.41	8.4(7.4-9.9)0.84	8.2(7.4-9.9)0.63	(n=18)
ED	1.7(1.4-2.1)0.25	1.2(0.8-1.3)0.20	0.7(0.6-0.9)0.12	1.2(0.6-2.1)0.46	(n=16)
EW	5.6(4.4-7.4)0.99	4.7(4.3-5.6)0.54	5.8(5.3-6.3)0.39	5.5(4.3-7.4)0.83	(n=15)
HW	8.8(8.2-9.6)0.59	7.2(6.6-8.3)0.59	7.8(7.4-9.3)0.54	7.9(6.6-9.6)0.81	(n=21)
PmW	5.7(4.1-7.9)1.42	4.7(4.0-5.2)0.52	5.7(4.4-6.9)0.75	5.4(4.0-7.9)1.01	(n=20)
DB	10.9(9.6-12.4)1.13	11.6(10.4-12.7)0.78	12.8(10.9-15.0)1.11	12.0(9.6-15.0)1.32	(n=19)
D-A	11.2(10.4-12.5)0.92	14.7(11.4-17.1)1.75	18.1(16.8-19.9)1.04	15.5(10.4-19.9)3.03	(n=21)
CPD	3.3(2.8-4.0)0.39	4.2(3.2-4.8)0.57	4.2(3.1-5.1)0.67	4.0(2.8-5.1)0.69	
CPL	11.9(10.0-13.9)1.35	12.6(11.1-14.8)1.17	14.3(13.1-15.5)0.79	13.3(10.0-15.5)1.50	
Sn-P	31.5(28.4-33.1)1.67	26.7(24.4-27.5)1.00	25.9(22.8-28.3)1.53	27.3(22.8-33.1)2.77	(n=21)
PL	7.8(6.3-8.8)0.92	7.2(5.3-9.8)1.19	6.9(5.8-7.4)0.59	7.3(5.3-9.8)1.19	(n=15)
Sn-D	58.1(55.3-60.1)1.79	53.8(51.1-55.7)1.39	53.0(50.5-56.4)1.82	54.4(50.5-60.1)2.67	
DB	30.2(28.1-32.5)1.55	36.3(33.3-38.1)1.58	35.5(32.9-37.2)1.24	34.5(28.1-38.1)2.74	
Sn-A	63.3(59.0-65.9)2.28	58.3(56.4-60.7)1.35	58.5(51.8-61.6)2.48	59.5(51.8-65.9)2.99	
AB	25.1(22.4-27.6)2.06	31.3(30.0-32.8)1.12	29.4(26.9-35.2)2.20	29.1(22.4-35.2)2.86	(n=21)
An-AO	1.6(1.3-2.2)0.31	1.6(1.1-2.1)0.30	1.5(1.0-1.8)0.27	1.6(1.0-2.2)0.30	(n=20)
CopL	15.5(n=1)	11.9(n=1)	13.1(11.8-14.1)1.28	13.2(11.8-14.3)1.43	(n=8)
CopL/W		44.0(n=1)	25.6(23.0-29.0)2.80	28.7(23.0-44.0)7.32	(n=7)
D	32.2(30-33)1.17	34.0(32-35)1.41	32.5(31-34)0.81	32.9(30-35)1.32	(n=21)
A	29.5(29-31)0.87	30.5(29-32)0.96	28.4(26-30)1.11	29.3(26-32)1.37	(n=20)

Table 9. Ranges of morphometrics, as % SL, and meristics of the genera of the Cetomimidae.

	Procetichthys	*Ditropichthys*	*Cetichthys*	*Notocetichthys*	*Danacetichthys*	*Cetostoma*	*Gyrinomimus*	*Cetomimus*	*Rhamphocetichthys*
n(SL)	1(236.5)	26(26.8-128.5)	12(51.5-196.2)	2(107.5-109.0)	6(34.0-53.9)	22(47.7-246.5)	60(51.0-358.5)	15(44.5-209.6)	4(90.8-125.7)
HL	30.2	29.1-34.9	31.2-38.5	31.3-31.9	35.3-37.7	22.3-31.4	25.8-36.6	29.2-43.1	34.9-38.1
SnL	11.2	9.4-14.4	10.9-14.3	10.8-12.5	11.3-12.7	7.9-12.5	7.1-13.9	10.8-15.5	16.2-19.5
PmL	25.0	19.2-23.4	22.7-29.4	21.1-22.3	29.0-31.4	15.4-23.5	20.9-31.2	22.6-36.4	25.8-32.0
LJL	25.4	19.8-23.3	20.7-29.6	20.6-21.2	27.6-32.1	15.9-24.7	20.6-30.7	23.4-38.8	28.2-34.9
Pm-Op	5.7	10.1-16.4	7.5-10.4	8.3-9.8	5.3-7.6	7.4-9.9	3.5-7.1	4.1-11.3	5.2-8.7
ED	1.1	1.0-2.2	0.7-1.9	1.0-1.4	2.0-2.4	0.6-2.1	0.5-1.9	0.8-2.3	1.4-1.7
EW	12.3	8.7-14.0	7.4-12.8	7.6-10.2	9.9-13.9	4.3-7.4	10.2-15.5	10.8-21.6	3.2-5.3
HW	9.5	8.2-17.3	13.4-19.8	11.4-12.9	14.5-22.0	6.6-9.6	8.1-15.1	9.7-22.6	7.5-13.2
PmW	13.1	11.4-16.6	9.4-16.6	10.7-13.8	11.8-16.7	4.0-7.9	7.4-18.2	5.6-24.7	7.5-8.8
BD	13.5	17.2-28.4	14.6-25.0	18.9-26.0	17.0-22.6	9.6-15.0	13.0-29.7	13.0-35.5	12.8-13.9
D-A	15.3	11.9-19.2	12.9-24.0	19.8-20.5	11.4-15.5	10.4-19.9	8.4-21.1	11.9-24.6	9.8-10.3
CPD	7.6	4.1-7.5	5.0-9.0	8.3-8.4	5.9-8.9	2.8-5.1	4.8-6.7	4.0-8.9	3.3-4.7
CPL	20.7	12.3-18.3	16.7-24.7	18.2-20.2	9.9-17.4	10.0-15.5	7.7-18.4	8.2-14.4	11.6-15.4
Sn-P	31.7	29.5-37.0	32.8-40.3	34.8-35.3	35.3-38.7	22.8-33.1	26.2-36.4	31.4-43.7	37.0-40.2
PL	11.0	8.2-15.0	5.2-10.6	7.7-11.9	8.2-13.4	5.3-9.8	3.4-9.4	5.2-15.8	8.0-12.2
Sn-D	66.4	63.2-68.7	61.0-74.0	68.5-69.7	67.6-73.5	50.5-60.1	65.7-78.0	67.0-79.3	71.6-75.7
DB	15.6	20.9-26.6	11.7-17.1	11.7	12.7-17.4	28.1-38.1	11.3-21.8	13.4-20.7	9.8-13.3
Sn-A	70.1	62.4-70.7	61.6-72.4	71.0-74.3	63.2-77.4	51.8-65.9	62.2-79.0	69.7-79.7	72.0-76.6
AB	12.7	15.1-19.8	7.1-14.3	9.9-10.6	11.6-17.1	22.4-35.2	11.0-20.9	10.5-20.5	9.1-12.5
An-AO	7.2	1.0-4.3	5.0-8.9	8.1-9.9	1.2-2.3	1.0-2.2	0.6-3.1	0.7-2.5	1.1-3.3
CopL	9.4	3.5-7.3	3.5-11.7	0.9-1.1	10.0-15.0	11.8-14.3	2.5-11.8	4.9-9.9	8.4-9.6
CopL/W	13.9	2.2-6.2	3.6-8.8	1.1-2.4	3.7-5.9	23-44	1.8-7.6	3.3-5.8	4.6-7.3
D	14	19-22	13-16	13	14-16	29-37	14-21	15-20	15-17
A	13	15-18	12-14	11-13	14-15	26-34	14-20	13-20	15-17
P	15	17-21	19-24	17-19	21-23	20-21	18-23	17-23	21-24
C	19	13-16	11-13	10-12	13-15?	(15)16-17	13-16	14-16	16-17
Vert	48	38-42	39-43	39-41	43-46	47-53	47-59	44-54	43-45
LLOr	86	10-13	8-14	15-16	16?-18	15-17	12-23	10-24	31-40
GRArch1	4+11-12	3-4+9-11	3+7-10	2+7-8	2+7-8	3-5+8-10	1-4+2-10	1+3-5	1-3+4-8

Table 10. Character state distribution in the Cetomimidae and outgroup genera *Barbourisia* and *Rondeletia*. Derived character states for computer analyses are marked *.

	Barbourisia	*Rondeletia*	*Procetichthys*	*Ditropichthys*	*Cetichthys*	*Notocetichthys*	*Danacetichthys*	*Cetostoma*	*Gyrinomimus*	*Cetomimus*	*Rhamphocetichthys*
1. Pelvic Fins	+	+	—*	—*	—*	—*	—*	—*	—*	—*	—*
2. Pleural Ribs	+	+	—*	—*	—*	—*	—*	—*	—*	—*	—*
3. D+A Rays	15-22	13-16	13-14	15-22	12-16	11-13	14-16	26-37*	14-21	13-20	15-17
4. P Rays	13-14	9-11	15	17-21*	19-24*	17-19*	21-23*	20-21*	18-23*	17-23*	21-24*
5. Principal C Rays	19	19	19	13-16*	11-13*	10-12*	13-15?*	15-17*	13-16*	14-16*	16*
6. Total Vertebrae	40-43	24-27	48*	38-42	39-43	39-41	43-46*	47-53*	47-59*	44-54*	43-45*
7. Preanal Vertebrae	16-19	9-12	20	20-24	24-26*	24-26*	26-29*	23-27*	26-40*	24-34*	27-29*
8. Lateral Line Organs	26-32	14-26	86*	10-13	8-14	15-16	16?-18	15-17	12-23	10-24	31-40*
- Lateral Line Form	CA	PA	PA	CA	CA	CA	CA	CA	CA	CA	PA
9. Snout Length % SL	11.5-12.7	16.2-21.8	11.2	9.4-14.4	10.9-14.3	10.8-12.5	11.3-12.7	7.9-12.5	7.1-13.9	10.8-15.5	16.2-19.5*
10. Eye Width % SL	11.8-14.8	18.4-19.9	12.3	8.7-14.0	7.4-12.8	7.6-10.2	9.9-13.9	4.3-7.3*	10.2-15.5	10.8-21.6	3.2-5.3*
- Snout to D Origin % SL	60.2-67.3	71.9-77.4	66.4	63.2-68.7	61.0-74.0	68.5-69.7	67.6-73.5	50.5-60.1*	65.7-78.0	67.0-79.3	71.6-75.7
- D Base % SL	23.6-31.4	17.0-22.9	15.6	20.9-26.6	11.7-17.1	11.7	12.7-17.4	28.1-38.1*	11.3-21.8	13.4-20.7	9.8-13.3
- A Base % SL	16.5-21.6	16.8-19.7	12.7	15.1-19.8	7.1-14.3	9.9-10.6	11.6-17.1	22.4-35.2*	11.0-20.9	10.5-20.5	9.1-12.5
- Anus - A Origin % SL	1.6-3.3	3.4-7.2	7.2	1.0-4.3	5.0-8.9	8.1-9.9	1.2-2.3	1.0-2.2	0.6-3.1	0.7-2.5	1.1-3.3
11. Cop. Tooth Plate Len. % SL	—	—	9.4	3.5-7.3	4.1-12.0	0.9-1.1*	10.0-15.0	11.8-14.3	2.5-11.8	4.9-9.9	8.4-9.6
- Cop. Tooth Plate Len./Wid.	—	—	13.9	2.2-6.2	3.6-8.8	1.1-2.4	3.7-5.9	23-44	1.8-7.6	3.3-5.8	4.1-7.3
12. Nasal Organ Devel.	++	+	++	—*	—*	—*	—*	—*	—*	—*	—*
13. Eye Lens Devel.	+	+	+	—*	—*	—*	+,—*	—*	—*	—*	—*
14. Head Canals	+	+	+	+	+	+	+	+	+	+	—*
15. Supraorbital Canal	1	1	1	1	1	1	2?*	2*	2*	2*	0
16. Dorsal Canal Pores	8	8	10*	9	8	10*	10?*	9	10-12*	11-12*	0
17. Infraorb. Canal	J	J	S*	J/S*	J	S*	S*	S*	S*	S*	0
18. Last Infraorb. Displaced	—	—	—	—	+*	++*	++*	—	++*	++*	0
19. Nasal-Infraorb.	—	—	+*	—	—	—	—	—	—	—	—
20. Jaw Teeth	CL	CL	W*	CL	CL	CL	CL	CL	CL	CL	CL
21. Jaw Tooth Rows	D	D	—	D	D	D	L*	D	L*	D	D
22. Vomer	Flat	Flat	Flat	Flat	Flat	—	Flat	Flat	Flat	Dome*	Flat
23. Palatine Teeth	—	—	+*	+*	—	—	+*	+*	+*	+*	+*
- Ectopt. Tooth Plate	Long	—	Long	Long	Short	—	Long	Long	Long	Long	Long
- Cop. Tooth Plates	—	—	1	1	1	1	1	3	1	1	1
24. 4th Gill Slit	+	+	+	+	+	+	+	Red*	—*	—*	—*
25. Pseudobranch	+	+	+	—*	—*	—*	—*	—*	—*	—*	—*
26. Holobr. Arches 1-3	L	L	L	L	S*	L	L	L	L	L	L
27. Holobr. Arch 4	L	L	L	L	S*	L	L	S*	L,S*	S*	L
28. Gill Raker Form	EL	EL	TE*	CL*	KN**	KN**	DP***	PL****	PL****	PL****	PL****
29. Gill "Rakers" Arches 2-3	+	+	+	+	+	+	+	+	+	+	—*
30. Medial Gill "Rakers"	+	+	—*	+	+	+	+	+	+,—*	+,—*	—*
31. Ven. Pharyn. Tooth Pl.	+	+	+	+,—*	—*	—*	+	—*	—*	—*	+
32. Lateral Line Scales	C,E	—	FL	FL	FL	FL	FL	FL	C,E*	C,E*	FL
33. Cavernous Tissue	—	—	—	AN+*	AN*	AN*	AN*	AN*	AN,AN+*	AN,AN+*	—
34. Subpectoral Organ	—	—	—	—	—	—	+*	+*	+,—*	+,—*	+*
35. Paired Abdom. Ridges	—	—	—	+*	—	—	—	—	—	—	—
36. Anal Lappets	—	—	—	+*	+,—*	—	—	+*	+,—*	—	+*
37. Anal Fin "Curtain"	—	—	—	—	—	—	—	+*	—	—	—
38. Stomach Pigment	+	+	—*	+	+	+	+	—*	+	+	Red
39. Peritoneal Pigment	+	Red	—*	+	+	+	+	Red	+	+	+

SOME LAPITA PEOPLE

Reber-Rakival Lapita Site, SAC locality, Watom Island. Rectangle III, base of Zone 4b, with burials 5 and 6 still in process of excavation.

14 DEC 1989

Preface

In 1985 the Department of Prehistory, Australian National University, Canberra, with additional funding from the National Geographic Society, Washington, USA, sponsored the Lapita Homeland Project in the Bismarck Archipelago of Papua New Guinea, under the main direction of Dr F.J. Allen, now Professor of Archaeology at La Trobe University, Melbourne. Among the many successes of that project was the re-excavation of the Lapita-period burial ground at Rakival Village, Watom Island, by Professor Roger Green (University of Auckland) and Dr Dimitri Anson (Otago Museum, Dunedin). Despite the fact that over 100 sites of the Lapita pottery phase of Western Pacific prehistory are now known, this Watom Island site is the only one with an associated burial ground that has yielded more than isolated bits of information about the *people* who made or used Lapita pottery, such as were previously available from the fragmentary materials found in Fiji, Tonga and the Mussau Islands of Papua New Guinea.

In 1986 Green, Anson and myself discussed putting together the results of our respective studies of the Watom site into a single volume. As the analyses of the skeletal remains from 1966 and 1985 progressed, it became apparent that these burials required special consideration. We decided to allocate them a separate publication in which they could be placed in a broader, regional context covering other Lapita skeletal remains known to that date. This is that separate publication.

It is almost a quarter of a century since the first Lapita burials were recovered. While many of our colleagues may regret that it has taken so long for basic data about those early discoveries to be made available, we believe that the delay has had its benefits. The developments in analytical and statistical techniques since that time, as well as major theoretical changes, allow a more comprehensive review of these important remains of prehistoric Pacific Islanders. Even so, the readers of this volume will soon realise that many central and fundamental questions about those early populations still cannot be answered unequivocally. Much remains to be done; particularly there is a need for additional comparative materials that will allow discussion of populations and not simply of individuals.

Our volume title has been deliberately selected. It draws attention back to a fundamental issue: what does 'Lapita' mean beyond a particular pottery style and other associated artefact forms? Authors often slide uncomfortably between the various nouns to which 'Lapita' is attached as an adjective - we find, for example, 'Lapita pottery', 'Lapita ceramic series', 'Lapita people', 'Lapita culture', and 'Lapita cultural complex'. We remain, by and large, ignorant about the *peoples* who made and/or used the Lapita pottery. Were they a uniform biological population? The answer must be sought through analysis of appropriate biological remains, and not through conventional assumptions imposed from the study of materials belonging to other disciplines. We must not expect the answer to be simple, neat and tidy. The papers in this volume reinforce this view.

JIM SPECHT

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Lapita People: an Introductory Context for Skeletal Materials Associated with Pottery of this Cultural Complex

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ABSTRACT. Various theoretical statements in the 1970's and 1980's by Howells, Bellwood, Pietrusewsky, Brace & Hinton, Terrell, and Houghton on the likely biological origins and affinities of populations which settled the geographic areas of Melanesia and Polynesia are outlined. They serve to highlight some of the background issues involved in a set of papers assembled here that constitutes the first thorough examination of human burials associated with the Lapita cultural complex. These are the only skeletal materials recovered so far from the Oceanic area to bear directly on the nature of the biological populations present in Island Melanesia and Western Polynesia 3,500 to 2,100 years ago and as such allow limited assessment of the different theories which to date have largely been derived from the analysis of either fairly recent palaeobiological evidence or from the study of still living populations.

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The discussion of the biological origins and affinities of the populations resident in Oceania at the time of European contact has a long history. It began with types called Melanesians, Micronesians and Polynesians, and it is in some ways unfortunate that those categories still remain with us today in many discussions of this topic. Certainly the concept of Polynesians as a reasonably homogeneous biological entity continues to have some utility (Howells, 1973:49, 228–233; 1979:282; Friedlaender, 1987:355–356) as it does culturally, linguistically and historically (Green, 1987; Kirch & Green, 1987). But this is emphatically not the case with the terms Melanesian and Micronesian, at least not in their original sense of separate and unified entities with a status similar to the situation in Polynesia (Terrell, 1986a: 15–41; Thomas, 1989; Green, 1989). In fact, as most researchers now recognise, the peoples of Melanesia in particular (i.e. those populations within the geographic area of New Guinea and Island Melanesia) are "...markedly heterogeneous in languages, customs and biology..." (Terrell, 1986b:195).

Above all, what has been evident from the time of Howells' surveys (1943:42; 1973:48) to the most recent compilation of biological data (whether of blood polymorphisms, anthropometrics, dermatoglyphics, odontometrics or other biological variables), "...is the extraordinary amount of biological diversity..." which characterises smaller areas within Melanesia (Rhoads & Friedlaender, 1987:125), as well as Melanesia itself. For this reason the phylogenetic relationships between the human populations of Melanesia, and those of Micronesia and Polynesia have been the subject of numerous formulations, none of them entirely satisfactory, and often not particularly congruent with those developed by the linguists and archaeologists for the peopling of this area.

This introductory essay focuses on some of the recent theories influencing these topics, especially in the field of anthropometrics and odontometrics, which serve as background to the set of papers assembled here, papers which constitute the first thorough examination of human burials associated with the Lapita cultural complex (Fig.1). It is hoped the papers of this volume will provide some limited assessment of those theories and perhaps suggest new views that can be evaluated in conjunction with those developed for the linguistic and archaeological evidence.

Linguists (Pawley, 1972; Clark, 1979) have now very systematically related the languages of Polynesia to a widespread Oceanic subgroup of the Austronesian (AN) language family in Melanesia and eastern Micronesia, which is but one family group among a total of some 60 odd unrelated language *families* (NAN) in that region (Foley, 1986:3). And archaeologists have convincingly traced the origins of the Polynesians and at least some later cultures in Melanesia and Eastern Micronesia back to an ancestral Lapita cultural complex widespread throughout Island Melanesia and Western Polynesia between 3,500 and 2,100 years ago. Yet similar results consistent with these views have not been an outcome of various endeavours in the area of biological anthropology. When the current views on the immediate origins of the Polynesians were first being developed, Green (1967:232), after reviewing some of the biological evidence, optimistically stated that "...it seems likely that populations once existed in more than one area of Eastern Melanesia from which one could derive both the Polynesians and a wide variety of populations that occur within Melanesia". But only a few years later Howells (1973:228), after a far more extensive review of all the biological evidence arrived at a quite different conclusion that "...the Polynesians – and the Fijians by and large are near them in body form – are simply too different from anything in Melanesia to be derived therefrom in a few thousand years". In his view they "...simply could not have emerged from any eastern Melanesian populations; they are just too different genetically..." (1973:234).

As the linguistic and archaeological evidence for the relatedness of ancestors of the Polynesians with groups in the Melanesian area grew stronger, Howells was inclined to modify his position as to the route of entry (see below). Nevertheless he still maintained that the biological pattern of his pre-Polynesians "...in external features – but above all in the cranium, is too positive to leave any reasonable suspicion of an ancestral connection with Melanesians, and in fact demands that the pre-Polynesians [whom he correlates with Lapita populations] had no important gene exchange with Melanesians before or enroute to their colonization of Polynesia proper..." (1979:283–284). His conclusion was that it was still possible to draw hypothetical arrows in too many directions; among the things required to limit the possibilities were Lapita skeletons, to resolve what was described as "...something of a dilemma...". Meeting this need with appropriate skeletal evidence and achieving its proper analysis has taken another decade, and even now the sample is extremely limited. However, further developments in the biological anthropology of Melanesia as well as this first small sample of skeletal materials bearing directly on the anthropometric and ondontometric nature of one group (Watom) and three separate individuals representing biological populations present in Island Melanesia and Western Polynesia 3,500 to 2,100 years ago allow some evaluation of the previous theories and the potential for development of new ones that better accommodate the various lines of evidence.

Melanesians as a Basic Population

A common position among many biological anthropologists in the Pacific has been that "...Melanesians

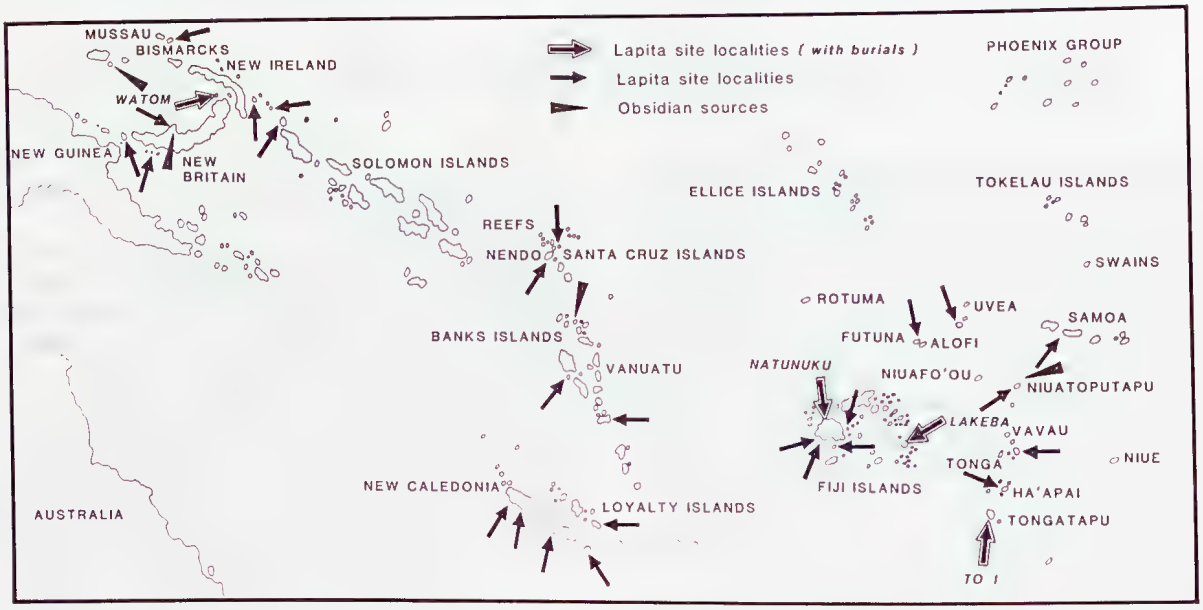

Fig.1. Distribution of Lapita sites in Oceania indicating those with burials.

are a single basic population rather than a composite, but a population of great genetic diversity..." (Howells, 1973:48). Swindler (1962:50) for example, following his study of some of the populations in Melanesia, found that they were sufficiently homogeneous to be regarded as a single geographical breeding unit. As Green observed this simply means that "...the various populations within this geographically delineated area have been exchanging genetic materials for a sufficient length of time to be more like each other than they are like groups outside this geographic area. It does not really help in establishing the origins of the basic populations which have contributed to its present makeup, for these may be the result of a long and complex history, nor does the fact that Melanesians are now somewhat like mean that the populations which now compose that unit were always so like..." (1967:230).

Given Howells' position of the Melanesians as a single basic population, and one that could not be in any significant way genetically related to Polynesians, it was necessary to devise an alternative formulation for the peopling of Polynesia. Initially this took the form of what I term a Melanesian avoidance theory, and involves getting ancestors of the Polynesians from Indonesia out to that area via a Micronesian route, with entry in this case via Eastern Island Melanesia and Fiji (Howells, 1973:252–260 and Figs 14a,b,c,d). Variations of this theory had been presented previously by Te Rangi Hiroa (Buck, 1944: 473, 520) and Duff (1959: 126–127; 1970:16). When the linguistic and archaeological evidence for a Melanesian origin and route became sufficient to discredit the Micronesian option, Howells had to suppose that somehow his pre-Polynesians "...reached the far end of the Lapita line (Samoa), however they entered it, without becoming physically Melanesianized to any significant extent along the way..." (1979: 284). This view is further developed in his introduction to the Solomon Islands Project volume (Howells, 1987:10).

Papers by others in that volume seriously challenge the view that all Melanesians constitute a single basic population, rather than a composite developed by a series of inputs, some major, some minor, extending over at least 40,000 years. Human colonisation of all of Ancient Near Oceania, comprising Sahulland or Greater Australia, plus the island groups of Wallacea, of the Bismarcks and the Solomon Islands chain, is now firmly established for the 30,000 to 40,000 year time range (Allen, 1989; Green, in press). Yet within that vast area, it is only from parts of the Australian zone that there is any fossil evidence which bears directly on what the initial *Homo sapiens* colonists may have looked like. Once Australia's indigenous populations were thought to have exhibited differences sufficient to talk of their multiple or "trihybrid" origins (Birdsell, 1949; 1967). Then, as the early skeletal evidence grew, opinion switched to the notion of two separate late Pleistocene groups, one gracile and perhaps from Asia, and the other robust and perhaps from Indonesia (Thorne, 1977; Wolpoff *et al.*, 1984:446) or more generally just from Sundaland (Howells, 1977). Other commentators, both in the past (Abbie, 1968) and recently, have failed to see in either the modern or fossil evidence really strong support for postulating more than a single founding biological population (Brown, 1987:62; Stringer & Andrews, 1988:1267). Howells, (1973:177) even went so far as to lump together all human populations over this entire area and extending into a source in Island Southeast Asia as "Old Melanesians", for which grouping Bellwood (1978:26; 1985:70, see also Fig. 3.12) has consistently used Coon's term "Australoids", while Oliver (1989:58) has recently referred to them as "Sundanoids".

In contrast to the implied homogeneity among Australia's aboriginal populations, those of Melanesia are consistently seen as much more heterogeneous and, while perhaps in some ways related to those of Australia, sufficiently distinctive to be separated from them. Detailed studies employing a wide range of observations across discrete biological systems suggest that populations in the Solomon Islands chain, and especially those on the island of Bougainville, consist of a number of quite separate biological populations. Thus for Bougainville, variation in blood polymorphisms and anthropometric measurements attest to two distinctive biological groups of "Papuan" or non-Austronesian speakers, one in the north of the island and another in the south (Rhoads & Friedlaender, 1987:153; Rhoads, 1987:168). More importantly in relation to our concerns, on a wider comparative canvass from New Guinea to the eastern Solomons, these data, together with odontometric and fingerprint comparisons (Froehlich, 1987:203; Harris & Bailit, 1987:257–258), separate the Melanesian Austronesian speakers from the non-Austronesians.

As a result of the fingerprint comparisons Froehlich (1987:204) concludes that "...from a broader perspective, the Melanesian evidence for an intrusive AN migration is unmistakable...". Other such comparisons suggest that "...biological similarities between New Guinea and Australia may reflect initial human colonization of Oceania...", while "...the distinctiveness of the Bougainville NAN populations may represent a subsequent migration..." (1987:207). Harris & Bailit (1987:259) also find that the odontometric patterns show "...that the NAN-speaking peoples of Bougainville Island have an origin and history in Oceania significantly different from that of more recent AN-speakers...". Friedlaender (1987:254–255) in his final overview on these matters, noted that on many biological characteristics the people of Bougainville are sufficiently set off from the populations of both Australia and New Guinea to indicate that the pre-Austronesian settlements in Island Melanesia are very old, a deduction now demonstrated to be true by recent archaeology. He added to this the prospect that they are also quite possibly the result of a number of separate migrations with subsequent differentiation *in situ* of a lesser magnitude. Taken together with his observation (Friedlaender, 1987:355) that the more recent "...Austronesian-speaking populations in Melanesia tend to show biological similarities in spite of their strong resemblances to immediately neighbouring groups...", an observation well supported by the most recent work on the gammaglobulin (Gm) distribution by Kelly (1988), it would appear that a number of reasonably distinct biological populations in fact occur in the Near Oceanic region of

Melanesia.

The question is, what are the relationships of these human populations to any fossil material that may be found in this region or those in the distant island groups of Remote Oceania. So far, unlike Australia, appropriate skeletal materials from the late Pleistocene are entirely lacking for Near Oceania (New Guinea, the Bismarcks and the Solomons) and not to be expected in Remote Oceania (the regions to the east of the Solomons settled only some 3,000 to 3,500 years ago). Thus the very limited set of Lapita skeletons assembled for study here, dating to between 3,500 and 2,100 years ago, are the first to cast any light on former populations in Melanesia and Polynesia at that time. Not surprisingly, various authors continue to interpret them in the context of present day populations, recent museum based skeletal collections and several of the more current theoretical positions used to explain such data.

Moving the Polynesian Ancestors through Melanesia

As indicated above, once archaeology and language made it evident that the Polynesians had their cultural and linguistic origins in Melanesia, this implied the same was probably true for their biological origins. New perspectives were required to accommodate this viewpoint. Avoidance theories now changed from postulating settlement routes that skirted Melanesia, to those which emphasised avoidance within Near Oceania of "Australoid" or "Old Melanesian" populations presumed to have been already long established residents. Thus Bellwood (1978:49) emphasised that the "...Polynesians and eastern Micronesians may have spread through Melanesia as a series of non-exogamous, sea-colonising groups, and that they did not come into very intensive genetic contact with the Melanesian populations...". Those who settled Polynesia and Micronesia retained much of their ancestral phenotype; those who remained in Melanesia became partially but not entirely absorbed.

Brace & Hinton (1981), working from the data of Oceanic tooth size variation, put forward a scheme very similar to that of Bellwood. They have an early large-toothed (megadont) pre-agricultural people whose eastern extent in the Pacific coincides with that for the settlement of Ancient Near Oceania (1981:fig.5). This is followed by a small-toothed population of Austronesian speakers, whose sophisticated sea-going technology enabled them to bypass the settled lands of South Asia and skirt much of New Guinea, the Bismarcks and the Solomons, but settle the previously unoccupied small islands of Remote Oceania, especially those of Micronesia and Polynesia (Brace & Hinton, 1981:557). On the way they inevitably met and mingled with the descendants of the earlier settlers of the large islands of Near Oceania. Some of these mixed populations later migrated into Remote Oceania as far as Fiji, Vanuatu, and New Caledonia.

In contrast to Brace & Hinton, Harris & Bailit (1987:242–243) find that megadont or large-toothed samples do not seem to extend east of New Guinea and that the Solomon Islands' populations they examined are seen to have small to medium dentitions with the NAN and AN speaking groups indistinguishable on this index. They (1987:258) conclude that "...except in extreme cases, size does little to disentangle the web of relationships, either just within the Solomons or in Oceania generally...". To them it appears that proportionality (shape), especially for individual tooth types, is probably a more indicative measure of a group's relationship than generalised size (Harris, 1981:559; see also Harris & Bailit, 1987:256).

Pietrusewsky (1977) examined crania from 17 separate populations in Oceania, (eight from Polynesia, seven from Melanesia and two from western Micronesia). Like Howells, he (1977:92) found a major distinction between groups in Melanesia and those of Polynesia, showing Fiji grouping with Melanesia on metrical traits and with the Polynesian, especially Tongan, samples on non-metrical traits (1977:94). Some affinities between the two western Micronesian samples and those of Melanesia were also noted, although cranio-metric results placed them within a Polynesian division (1977:94). Since this paper was published, as Pietrusewsky (1989) notes in the summary to his study of the Natunuku Lapita skeleton a long list of additional papers, both by himself and others (based on a wealth of evidence covering anthropometric data, cranial variation, genetic data, and dentitions of numerous Pacific populations), have all identified the Polynesians as genetically uniform and unrelated to the Melanesians. His cautious reconsiderations here, based the sample of 11 Lapita specimens which lead him to reopen that question, deserve careful appraisal.

Deriving Polynesians from Palaeopopulations in Melanesia

The position that it was biologically impossible to derive Polynesians from Melanesians, or that there were *no* populations, now or in the past, in Melanesia which could be ancestral to both Polynesians and some of the diverse populations in Melanesia was never one to which either Houghton or Terrell were attracted. Houghton (1980:73) simply saw the first Polynesians as "...a canoe-load of closely-related people cast upon the then uninhabited Fiji, not at all typical of the populations from which they sprang...plucked by drift of genes and canoes out of the populations inhabiting island Melanesia some four thousand years ago". For him, the answers lay in the ground, and what was required was human skeletal material in association with Lapita pottery (1980:71). At that time he had studied only one such specimen, from Lakeba in the Lau Group of Fiji, which he assessed as a person fully Polynesian in physical form. Now the samples Houghton has examined also include a specimen from Tonga, and the eight from Watom. The model within which he works is not all that different from the one originally proposed, namely that the dominant settlement of Polynesia was by a small group drawn from one of the varied populations of Island

Melanesia.

Such a model was given a fuller and more theoretical treatment by Terrell (1986b). He too envisages the departure of a small, genealogically-biased sample of people from a genetically heterogeneous prehistoric Melanesian source population comprised of numerous local entities. This population then undergoes immigrant selection for large body size and other characteristics, including those that favour survival on long sea journeys, resulting in colonisation of previously uninhabited island groups. This is followed by population growth, settlement expansion and local differentiation, plus periodic in-migration from the original Melanesian source population. The result is numerous geographically differentiated local populations in the region comprising the Fiji, Tonga and Samoan triangle. According to Terrell (1986b:196) the processes involved are lineal fission, immigrant selection, and isolation-by-density. These are invoked to explain how biologically homogeneous Polynesians emerged from more diverse palaeopopulations located somewhere in Melanesia. What was lacking, of course, were suitable skeletal remains from Lapita and early Polynesian sites that might lend support to this particular model.

Other Issues

Diet. In addition to the various assessments of biological affinities, several authors in this volume comment on health and dietary conditions exhibited by these skeletons or their teeth. The open question in respect of diet for Lapita has been the degree to which horticultural or land based resources, versus those of marine origin, were important in the economy. Several separate studies, not included here, have addressed these questions in respect of some of the human remains under examination in this volume.

Evans (1987, in press) has addressed the incidence of dental caries and diet in a number of prehistoric Oceanic populations, including those of Watom and Lakeba. In both the latter cases the number of teeth, 24 and 22 respectively, are few, and the incidence carious 0.000% and 31.82±16.8% quite markedly different. Given the bias possible from the effects of sample size they are not easily interpreted in respect to diet.

More useful is the work of Horwood (1988, 1989) on trace element analysis of human bone from several prehistoric Pacific Island skeletal assemblages including Watom. Her conclusion (1988:138) was that the low zinc values combined with the high normalised strontium value can be interpreted as an indication that these people were consuming proportionally more vegetable than meat foods in their diet. The focus of the diet was predominantly terrestrial, rather than marine (Horwood, 1988:153).

Work underway by Quinn (Appendix 4 in Horwood, 1988; see also tables 1 to 3 in Leach *et al.*, in press), uses nitrogen, carbon, and sulphur isotope analysis to bear on this problem. Again the Watom sample is found to have a mixed terrestrial and marine diet, with the terrestrial component being of greater significance than would be expected for "strandloopers". The nitrogen values indicate a marine component derived mainly from a reef environment. Results for the To.1 skeleton are not too different from those of Watom (Leach *et al.*, in press).

Differences in measurements between three authors. It will be apparent to the careful reader that in some observations common to two or, with respect to teeth, three of the authors, that not only are differing points of view expressed after examining the same evidence, but observer differences also occur in the records for various of the measurements obtained. Some of the inter-observer variation may well be due to the poor state of the skeletal remains themselves, but in addition it raises the problem of the degree of standardisation achieved in measurement procedures. It also poses the question of the degree to which these differences might effect the various analyses employed. Still, it is important to recognise that the various articles in this volume present for the first time a great deal of detailed biological data on the known though limited range of Lapita skeletal material which has been recovered. Future studies will doubtless address some of the observational and analytical problems that they raise and examine such data in new frameworks.

Dating and context. A small and miscellaneous collection of fragmented skeletal and often isolated dental remains from Lapita sites in the Mussau Islands has recently been published (Kirch *et al.*, 1989) which allows some very preliminary observations to be drawn about early Lapita people in that region. They suggest these people had slightly closer affinities with Indonesian than with Melanesian populations. In this context the Watom skeletal collection of eight individuals becomes an important sample as it is rather more representative of a single population and provides somewhat fuller data on their skeletal and dental characteristics. However, in relation to its chronological position, it is located towards the end of the Lapita sequence, some 40 generations (or 1,000 years) after the Lapita cultural complex first appeared in the Bismarck Archipelago 3,500 years ago. In contrast the three individual skeletons from Natunuku in Fiji, from Lakeba in Fiji's Lau Group, and from To.1 in Tonga, reflect the earlier and middle part of the Eastern Lapita sequence. Here it is thought Lapita people were the first inhabitants, whereas in the islands of the Bismarck Archipelago, people of uncertain affinity had been resident for 35,000 years or more, and the Watom and Mussau samples and their different dates requires that situation also to be taken into account.

Conclusion

No concluding essay appears after the last of the papers presented in this volume. Rather, authors of each of the articles arrive at separate, sometimes contrastive, and usually tentative results. Sample sizes are still too small for it to be otherwise. Moreover, the several theoretical and

analytical frameworks within which this first assemblage of detailed biological data on Lapita skeletal material is interpreted are not such as to warrant drawing firm summary conclusions. Instead, what one hopes is accomplished is that some of the present conceptual frameworks in which the peopling of this part of the Pacific have been formulated will now be re-examined and in due course replaced by new propositions that accommodate better the ever increasing body of new biological evidence.

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The SAC Burial Ground, Watom Island, Papua New Guinea

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ABSTRACT. Discussion of the burial practices associated with the Lapita cultural complex has previously been limited through lack of evidence. This is rectified by presenting the basic mortuary data on a sample of eight adult inhumations from the SAC burial ground in the Reber-Rakival Lapita site on Watom Island and comparing them with three individual burials from Lapita sites in Fiji and Tonga. A common preference for burial in flexed positions within a small rounded pit feature is evident in the sample, although this practice does not apply to every case. There is, however, less consistency in orientation of the body, the greatest number being with the head to the west.

GREEN, R.C., D. ANSON & J. SPECHT, 1989. The SAC burial ground, Watom Island, Papua New Guinea. Records of the Australian Museum 41(3): 215–221.

In Green's (1979) review of the Lapita cultural complex, little discussion of associated human burials was possible because the known examples were so few: Reber-Rakival, Watom; Natunuku, Fiji; To.1, Tonga. Among these only the locality of SAC (then site 8 or FAC) at Reber-Rakival on Watom Island, East New Britain Province, Papua New Guinea, suggested that an area within a site contained a possible burial ground. It was here that Specht (1968:126) described three burials located in trench I within an area of 6m^2, in the lower-most occupation zone designated C2. A direct date on a bone sample from parts of the three roughly contemporary burials yielded a result of 2,420±110 B.C. (ANU-37b) (Specht, 1968:124). As part of the Lapita Homeland Project (Allen, 1984), Green and Anson with the initial assistance of Specht returned to Watom Island and the Reber-Rakival site with several objectives. One of these was to recover further Lapita-associated burial material by exposing a larger area at the SAC locality, one of several localities investigated within the Reber-Rakival area (Fig.1). Thus the SAC Watom excavations represent the first recorded investigations of a burial ground associated with the Lapita cultural complex. The other three burials dealt with in this volume are each individual cases from separate sites in Fiji and Tonga (see below). Other objectives were aimed at gaining stratigraphically secure radiocarbon samples which would help to pin down the chronological ages of the various occupation deposits associated with Lapita pottery on Watom and confirm the postulated late position of these among Lapita assemblages assigned to Far Western region (Anson, 1983, 1986).

An outline of some of the results from the excavations

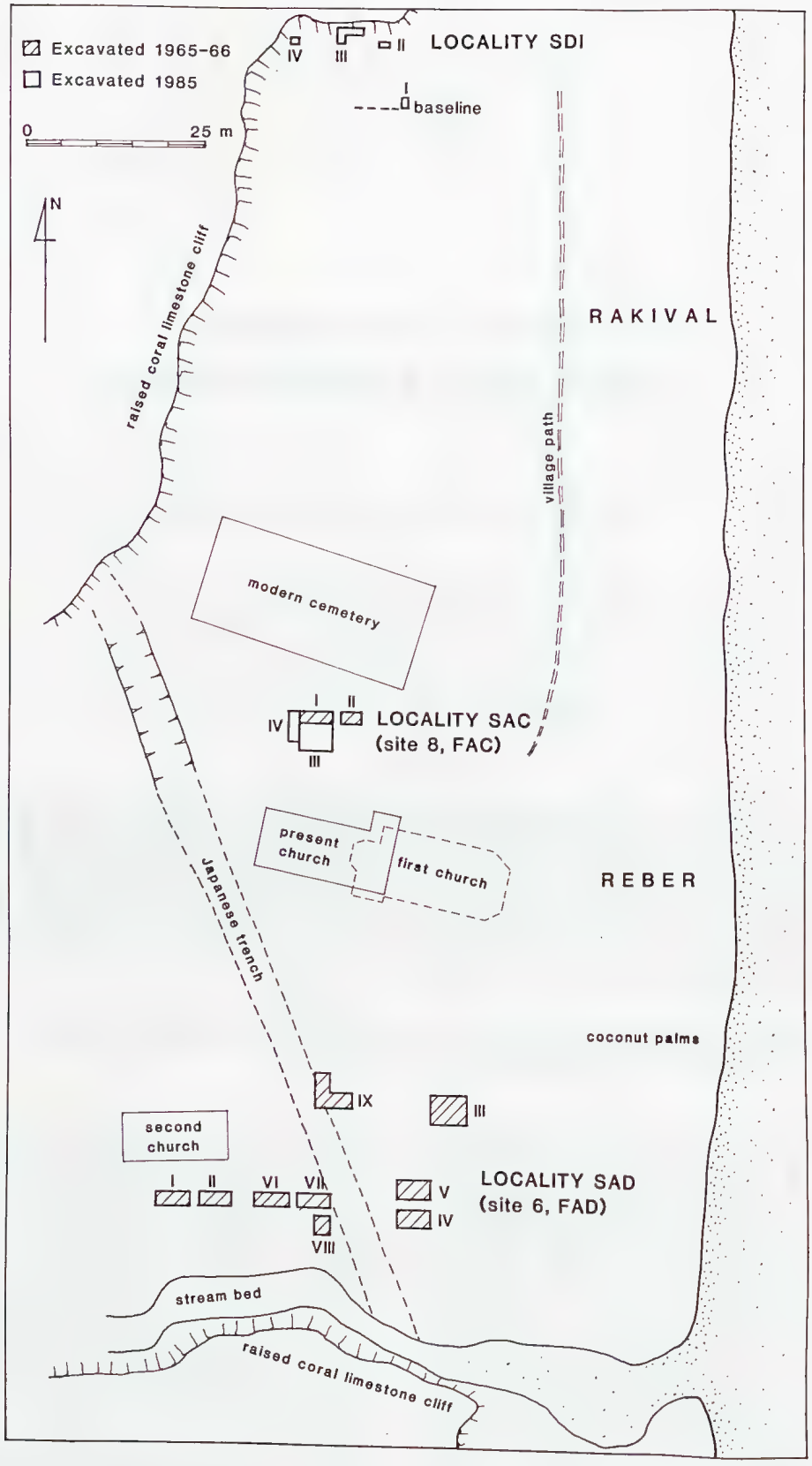

Fig.1. Map with excavation localities in the Reber-Rakival village area on the island of Watom, East New Britain Province, Papua New Guinea.

conducted on Watom in 1985 has already been published (Green & Anson, 1987). The excavations allowed us to define a sequence of occupation at the SAC locality which supports and expands on Specht's initial observations. They also furnished shell samples yielding a series of radiocarbon determinations which permit more precise dating of the deposits. The present report provides fuller information on the stratigraphic and chronological contexts of the three burials found by Specht and the five additional burials recovered by Green and Anson. It also describes the plan of the burial ground and the position and nature of the inhumations that occur there, to furnish a context for the description and analyses of the human remains that are the subject of subsequent papers in this volume.

Stratigraphic Sequence and Chronological Age

Specht's (1968:123) description of the SAC stratigraphy is fully confirmed by our excavations. They demonstrate that there were two Lapita cultural deposits underlying a primary volcanic ash from the Rabaul eruption dated to between the 7th and 9th century A.D. (Walker *et al.*, 1981:186; Green & Anson, 1987:123). Overlying the primary ash are thick deposits of secondary ash and more recent material. The lower cultural deposit is a grey sandy layer labelled by Specht as zone C2. It is now dated by two calibrated determinations on a shell sample from its base to the first four to five centuries B.C. (Green & Anson, 1987:124). The initial occupation associated with zone C2 appears to have been residential in function (see below). Subsequently this part of the Reber-Rakival site was converted to a burial ground. All inhumations are within this deposit, with some features extending down into the coralline beach sand at the base of the site. Although no further dates have been obtained for the upper part of zone C2, a 500 to 100 B.C. age is entirely consistent with the previous date on the bones themselves, and the date for a shell at the base of the layer above.

The upper cultural deposit is a black loam layer labelled by Specht as zone C1. It everywhere seals in zone C2, and at its base sometimes exhibits truncated features intruded into zone C2. These features, as well as a greater quantity of Lapita pottery and other cultural items in the deposit, indicate that the locality returned to residential use at this time. The deposit is dated by a shell sample from the base of zone C1 which, when calibrated, gives an age that probably lies between the first few centuries B.C. and the first few centuries A.D. (Green & Anson, 1987:124). In the final stage before the ashfall, the upper black loam layer appears to represent gardening activity that formed a palaeosol when it was sealed by the ash of the Rabaul eruption. Our opinion is that the inhumations in zone C2 constitute the only stratigraphically well defined and securely dated burial complex of the Lapita cultural complex.

Layout of the Burial Ground

The total surface area of cultural deposits exposed at locality SAC now covers some 42m^2. These allow us to define a set of structural features associated with the zone C2 deposit (Fig.2). From subsurface coring carried out by C.A. Key at the time of Specht's excavations, we know the initial Lapita occupation at this locality was on a well drained coralline beach flat with a low lying dune just behind. The first thing of note is that in Specht's rectangle II, very few features were encountered, and no burial material. Based on profiles in relation to present sea level, this very low lying portion of the site towards the present day beach must in the past have been much closer to the tidal zone. Inland of this in rectangles I and III is a low coral block and igneous stone alignment running parallel to the beach in a north-south direction. In some instances it overlay pits and postholes from an initial residentially-oriented occupation. To the west and inland of this alignment all eight burials were located within a fairly compact area. The alignment appears to be part of the a boundary wall associated with the burials as both are late features within zone C2. It seems likely that it once formed an enclosure.

Specht located and fully excavated the first three burials in rectangle I, but through lack of time was then unable to complete excavation of the entire rectangle. Anson and Green removed the backfill down to the plastic which he had left at its base (with the intent of returning later), and continued to define the remaining structural features. This lead to the discovery of portions of three additional burial features, which extended either into rectangle III to the south or rectangle IV to the west. Two other burials were found, one close to this cluster, partly in rectangle III and partly in rectangle IV, while the last was somewhat to the south in rectangle III. The total area excavated was too small to define the full extent of the burial ground, or additional inhumations that may have lain within its confines.

Inhumations

It seems likely that gardening activities to a depth of circa 30cm turned over and incorporated into zone C1 a small amount of pottery, obsidian, bone and other material from the top of zone C2. This is consistent with the evidence for disturbance of some of the skeletal material, fragments of which extended into the upper part of zone C2 and occasionally into the lower spit of zone C1. As a result of this rather random activity, some of the skeletal remains, such as those from burial 2, were very disturbed and fragmentary, while in other cases such as burial 6, the skeleton was largely complete and in articulation. The other difficulty encountered was that burial features often extended down into the underlying sand beach to within the tidal zone and on a daily basis filled with water. This meant that nearly all the human bone was wet, soft and difficult to remove intact; or, when excavated, difficult to

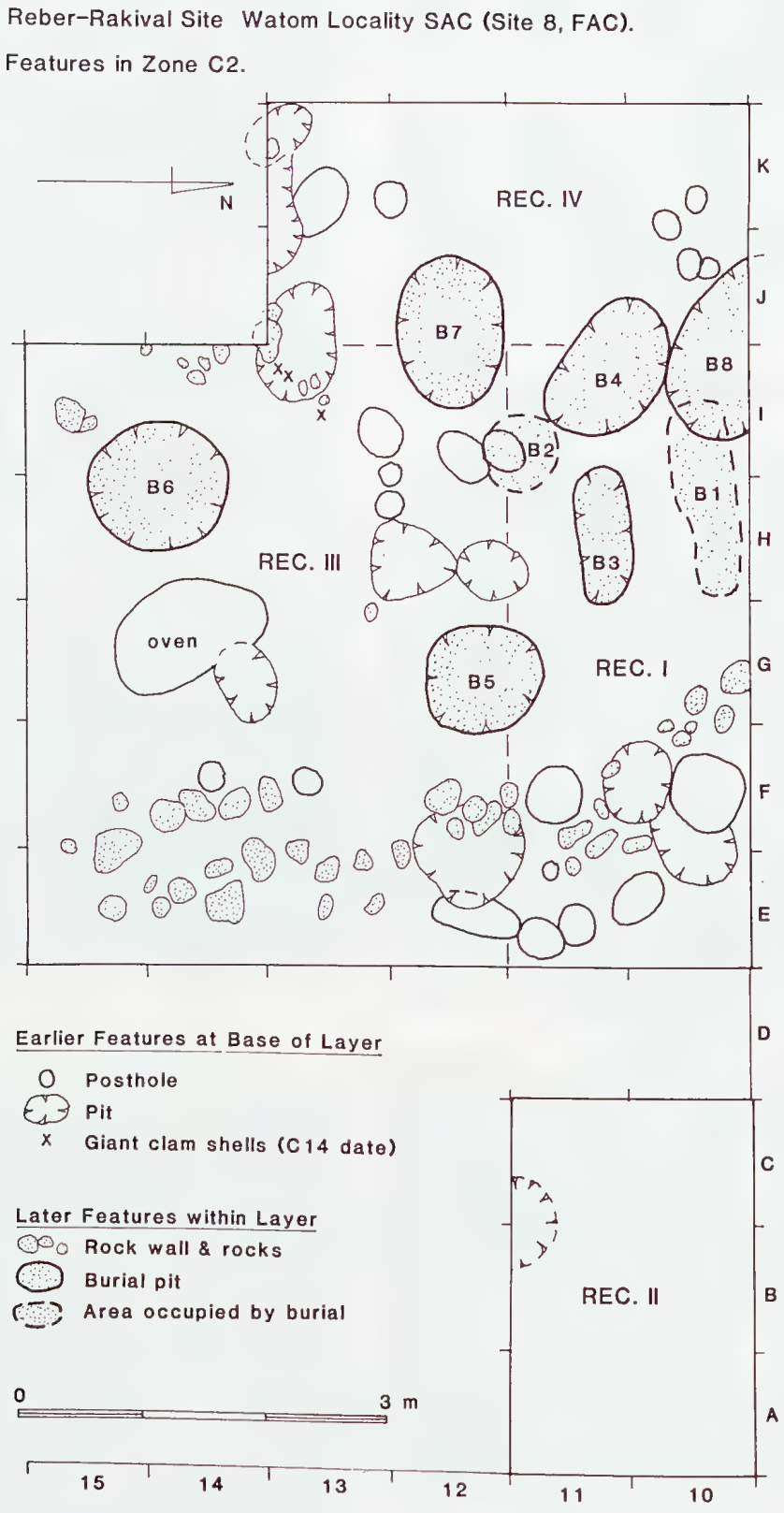

Fig. 2. Plan of features including burial pits at base of zone C2 in the SAC locality of the Reber-Rakival Lapita site on Watom Island.

dry and harden.

As Specht (1968:126) was unable to detect or define a pit for burial 1, it is possible only to indicate the area in which that skeleton lay. Inhumation presumably consisted merely of covering the body with earth. For all other burials, pits or parts of pit features could be defined. This may be significant as only burial 1 was in a fully extended and supine position. There was no skull, though a slab of igneous rock was placed where the skull ought to have been and the body had been oriented with its shoulders to the west and its feet to the east. All the other inhumations were in oval to rounded pit features, suited in size to either bundle burial or placement of the body in a flexed position.

Three burials, each in a pit feature, were definitely in tightly flexed positions. Burial 3, excavated by Specht, was a reasonably complete skeleton placed on its back in a supine flexed position. The body had been interred with the head to the west but turned to face north. In burial 4, although the skull was missing, the position of the arm, leg and pelvic bones indicated that this too had been a supine flexed inhumation where the body had been placed on its back with shoulders to the west. Burial 6, which consisted of a nearly complete skeleton, was lying in a seated flexed position on its back. In this case the body had apparently been positioned with shoulders to the south. The skull, however, had dropped forward to the north.

Burial 2 was initially represented by bones of the lower body (Specht, 1968:126) and additional excavation recovered only a few more fragments from the infracranial portion of the skeleton. Green and Anson were able to demonstrate, however, that inhumation had occurred in a pit feature which appeared to cut away the upper part of an earlier posthole at its base. Specht believed burial 2, with its somewhat scattered bone, had been disturbed by burial 3, a point we were unable to confirm. The burial 5 pit also sealed in or cut through earlier features. Few bones from it occurred in rectangle I, and those in rectangle III were generally not articulated but remained in a pile towards the central part of the pit. It had no skull and only fragments representing other parts of the skeleton. In rectangle III burial 7 consisted of a few leg and feet bones plus some vertebral material and cranial fragments. Definition of the upper part of the skeleton proved difficult when excavation was extended into rectangle IV, although further bones from that portion of the body were recovered. Bits of scattered human bone, including part of a mandible and portions of a cranium plus a scapula, were found scattered in the squares to the west of the burials in rectangle IV. Some skeletal fragments were found within the first spit of the sandy grey deposit of zone C2 and may be disturbed remains from burials 4 or 7. Similar bone material, including a second mandible, was found in spit 2 of zone C2 just west of burial 8.

In rectangle IV articulated portions of the upper limb bones were found in burial pit 7, while in burial pit 8 the lower limbs, a few bits of skull, several teeth, scapula and vertebrae were found among many fragmentary bones. However, in neither case could we identify a fully complete and articulated human skeleton.

In respect to modes of inhumation, two categories plus a set of disturbed remains can be identified. The first, represented by burial 1, is an articulated, extended supine inhumation without a skull and not in a pit feature, which is unique. The second is the articulated flexed burial in an oval to rounded pit, represented by burials 3, 4 and 6. The lack of a head in the case of burial 4 appears to us to be the result of post-depositional disturbance in antiquity. This view is supported by Pietrusewsky (1989a) on the basis of the presence of the atlas vertebra. We believe other skeletal fragments, including a mandible found in the grey C2 zone deposits to the west of this burial, are probably some of the pieces missing from that skeleton.

The third grouping includes burials 2, 5, 7 and 8. In all these cases the excavations recovered incomplete skeletons, and only occasionally were the bones in positions of articulation. Several interpretations can be offered for this. One is that these inhumations represent incomplete secondary bundle burials. While burial 5 could possibly be such a case, this certainly does not appear to be the situation with respect to the other three, where some articulation was in evidence and subsequent disturbance in antiquity is a more likely factor. Thus our impression is that burial 7, which included some cranial material, was originally in a position very similar to burial 4. Burial 8 may also have been of this type. Finally burial 2, clearly disturbed in antiquity, exhibits enough articulation among the few remaining bones not to support a secondary or bundle burial option. That leaves only burial 5. Here the pit base extended well below the high tide level, so that bone preservation was extremely poor; the fragmentation plus problems in excavation made it difficult to judge the degree of articulation.

Leaving the secondary or bundle burial option as an unlikely interpretation for burials 2, 5, 7 and 8, the deliberate disturbance of a primary burial in antiquity could still apply to burials 2 and 8. Here the evidence of an incomplete, semi-articulated skeleton could imply partial disinterment following primary burial and subsequent decay of flesh and ligaments, making possible the later removal of some bones and especially those of the skull. Such an interpretation, while not impossible, is more difficult to apply to burial 7 where fewer bones are missing. For burial 5 the evidence does not allow a choice between this practice and a secondary burial option.

The postulation of secondary or of deliberately disturbed primary burial has to be balanced against a more general explanation involving all burials, namely that of later disturbance and loss or removal of a variety of skeletal parts through more random activities. This would have occurred after the locality was abandoned for burial purposes and again used first for residential and then gardening functions. The result is that there are no complete and fully articulated skeletons present and a wide range of bones is in fact missing. It is this last interpretation which we favour.

Bones of a very young child (one to two years) from Specht's excavations were found by Houghton among the 'miscellaneous bones'. They were not identified at the time of excavation and Specht is of the view that they may be from the post-Lapita child of site 6 or SAD (1968:122). Their

stratigraphic context and association with SAC is uncertain.

The orientation of the burials suggest that one preferred mode for the placement of dead was with the head to west. In this category the evidence from burials 1, 3, 4, and probably 7 seems fairly clear. In the case of burial 6, it would appear the torso lay to the south and the head had tipped forward. No statements are possible for the other burials, except 8, where a jaw, which perhaps may be associated with this skeleton, was found in the zone C2 deposit to the west of the burial pit.

Grave pits in general contained no obvious burial goods. Three contained seemingly associated volcanic stones. Exceptions could be parts of an undecorated shell-tempered pot in burial 5, along with some pieces of classic dentate-stamped ware, and the shank of a shell fish hook with burial 4. However, it is clear that neither whole pots nor other important funerary items were placed in the burial pits, as concentration of sherds or other portable artefacts did not occur in these features.

Comparisons with Other Lapita Burials

The only primary burial known from the Lapita period of Tonga, the AK burial, was placed in pit AF of Trench III in site To.1, Tongatapu. While it is not certain that the pit was originally dug for this purpose, due to the layer of red-burned soil in its lower part, it was in the end used as a grave (Poulsen, 1987:21). 'The body was placed with back on the ground, head towards the west, elbows close to the body with the knees up by the left hand' (Poulsen, 1987:22). This unnatural posture is an indication that the body was probably bound in this position, but not because of the small size of the pit, since there was space between the skeleton and pit walls. Disturbance of the fill in the upper part of the pit took place at a considerably later time, removing some major bones of the right leg (Poulsen, 1987:22; Spennemann, 1987:290). A small shell adze was placed at the right elbow, apparently as a grave gift (Poulsen, 1987:22).

A primary Lapita period burial from Lakeba in the Lau Group of Fiji occurred at 800 mm depth resting on a cemented layer of grey to orange sand in Trench 28 of site 196 (Best, 1984:100). There was no evidence for an associated pit feature and pottery from the excavation unit around and immediately above the burial fitted in well with that from the units assigned to the lower deposit but not with those above (Best, 1984:221). In addition, two other groups of human bones, both from very incomplete skeletons, were found below this level (Best, 1984:100 and Fig. 7.9 right).

In the Natunuku area of Viti Levu, Fiji one adult skeleton showing little disturbance lay in a crouched position in a shallow grave in layer 5a at locality C of site VL1/1 (Green, 1979:55; Pietrusewsky, 1989b). The skull faced north. Little more information is available, as the site report is unpublished.

The lack of any obvious pit feature containing the site 196 Lapita burial on Lakeba parallels the situation of burial 1 at SAC on Watom. In the two cases of Tongatapu and Viti Levu the flexed burials are placed in small oval pits as at SAC Watom. The flexed-on-back position of the To.1 skeleton seems most similar to those of SAC Watom burials 3, 4 and 6. While the burial from Lakeba on its side has no obvious parallel, the individual burials for the two other Lapita sites used various flexed positions as at SAC Watom. Only one of them, however, (To.1 from Tonga) exhibits the head to the west position favoured in Watom. Except for an adze in the To.1 burial, grave goods did not feature as part of the burial ritual.

Conclusion

The SAC locality at the Reber-Rakival site on Watom constitutes a securely dated though disturbed set of inhumations assignable to the late period of the Lapita cultural complex. Despite the 79 to 100 Lapita sites now known, and the 49 or so now investigated through excavation (Kirch & Hunt, 1988: 15–17), little information on Lapita burial practices has been forthcoming. However, it is now possible to say that one of the common inhumation practices was focussed on flexed burial, usually within a pit, and with the head often oriented towards the west. Because few inhumations from Lapita sites have been reported, there has been continuing speculation about where people from the Lapita cultural complex were buried. An answer is that they were sometimes buried within large Lapita settlements in a distinct burial ground complex, and at others in more individual circumstances. The problem we face is one of adequately sampling large Lapita sites through the use of excavation strategies that expose all of the different activity areas involved.

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Watom: the People

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ABSTRACT. The human material from the Reber-Rakival Lapita site on Watom Island has been analysed. Eight adults and a two year old child are defined in addition to scattered adult material. Mean age at death of the adults, comprising two females and six males, was about 30 years. Mean stature of three males was 1,784 mm, and that of a female was 1,659 mm. Long bones were moderately robust, and bowed to accommodate a considerable musculature. One substantially-complete mandible showed Polynesian 'rocker' characteristics, and it is probable that two adult mandibular fragments shared this morphology. Another substantially-complete mandible, though very robust, did not show this form. The morphology of this group displays the large-bodied characteristics of oceanic voyagers and small-island dwellers. Statistical analyses of mandibular and dental metric data support the morphological evidence of affinities with prehistoric Polynesians of rather later date.

HOUGHTON, P., 1989. Watom: the people. Records of the Australian Museum 41(3): 223–233.

Material

This paper discusses the human remains from locality SAC at Reber-Rakival on Watom Island.

The human remains were recovered from Rectangles I, III and IV, during two separate excavations, in 1966 and in 1985 (Specht, 1968; Green & Anson, 1987; see also Green, Anson & Specht. this volume). The 1966 excavation identified three individuals from Rectangle I. The 1985 excavation identified a further five individuals from Rectangles III and IV, and in addition recovered an amount of dispersed human bone from Rectangle IV. The material thus comprised the incomplete remains of eight individuals recognised at excavation, and mixed material from Rectangle IV that could neither be clearly assigned to any of the recognised individuals, nor ascribed to another single person. In addition, remains of another discrete individual from Rectangle I were identified in the laboratory.

In general the remains are incomplete and broken, and the bone, having been exposed to the fluctuations of tidal sea water through the soil, is poorly preserved.

Methods

Ageing was done by standard biological criteria of maturation or degeneration. However, the very scanty skeletal representation means that for most individuals the age estimate is only an informed guess. The bone was unsuitable for histological methods of ageing. Sexing was based on pelvic morphology wherever possible, and was supplemented by citrate analysis (Dennison, 1979), which allowed sexing of all adults. Stature was assessed from overall lengths of long bones, or segments of bone. Two sets of estimates were made, using the formulae of Trotter (1970) derived for white Americans, and those of Houghton *et al.* (1975) for Polynesians. Standard metric data were

obtained from long bones and mandibles, and the occurrence of certain morphological characters was noted. Shape and size of teeth were recorded. Cortical thicknesses of second metacarpals were assessed from radiographs. All material was examined for evidence of bony or dental pathology. Multivariate statistics (Penrose Size and Shape) were applied to mandible and tooth data to investigate possible biological relationships of the group.

Findings

Individual findings are detailed in the census, Appendix A.

Age. The estimates are set out in Table 1, together with the method used. With the exception of the young child, all were adults, with an average age at death probably a little over 30 years.

Table 1. Age of Watom individuals, and criteria used in assessment.

Individual	Age (years)	Criteria
1	mature adult	full epiphyseal union
2	20	left fifth metacarpal shows a fusing epiphysis
3	25-30	rounded tooth roots, minimal joint degeneration
4	30+	degeneration of lumbar vertebrae
5	30+	slight lipping of vertebral bodies, and costo-chondral junction
6	mature adult	full epiphyseal union
7	25+	mature bone
8	25+	vertebral lipping
child	2	length of tibial diaphysis

Sex. Table 2 gives the sex of the individuals and the gross morphology used to establish this. Citrate assay supported the gross assessments. There were two women and six men in the group.

Table 2. Sex of Watom individuals, and morphological criteria; all estimates were supported by citrate analysis (Dennison, 1979).

Individual	sex	morphological criteria
1	female	pelvis
2	female	nil
3	male	pelvis
4	male	pelvis
5	male	pelvis
6	male	general size and morphology
7	male	nil
8	male	nil

Skeletal morphology and measurements. *(a) Crania.* An attempt was made to reconstruct the cranial fragments of individual 3 but postmortem distortion rendered this impossible. The only data obtained were the median sagittal arcs for frontal (106 mm), parietal (107 mm) and occipital (88 mm) bones.

(b) Mandibles. For individuals 3 and 6 fairly complete reconstruction of the mandible was achieved. Two further incomplete bones were recovered from the scattered Rectangle IV material. The bones were robust, with strong basal portions and particularly for individual 6 a very broad and high ramus. The mandible of individual 3 (Fig.1) was of an unequivocal rocker form, the two incomplete bones were probably of this form (Fig.2), while the mandible of individual 6 (Fig. 3) was not of the rocker form. Standard metric data on the two more complete bones are set out in Table 3.

(c) Infracranial skeleton. Few bones were intact and observations were limited. The long bones generally were

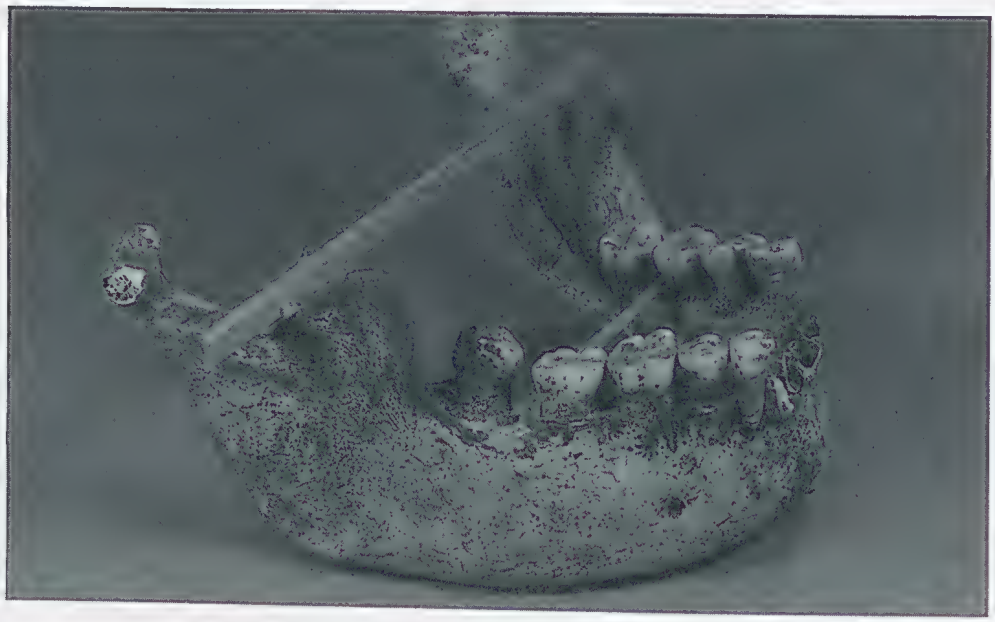

Fig.1. Reconstructed mandible of individual 3.

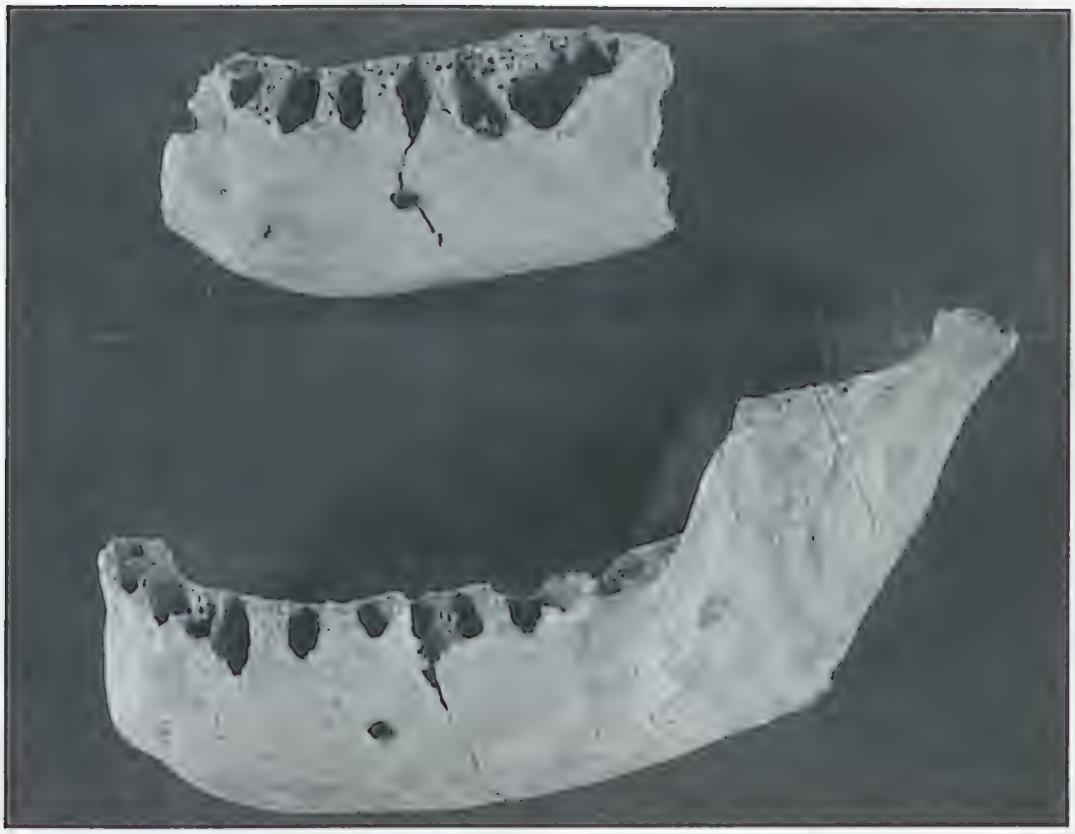

Fig.2. Two mandibular fragments from Rectangle IV. It is probable that both were of 'rocker' morphology.

Fig.3. Reconstructed mandible of individual 6.

robust, and bowed to accommodate a considerable musculature. Metric data are in Appendix A.

Stature was estimated from the lengths of long bones . Table 4 gives stature in millimetres of the four assessable individuals using both white American equations (Trotter, 1970) and Polynesian equations (Houghton *et al.*, 1975). The Polynesian equations gave the female a stature of 1659 mm and a mean for the males of about 1784 mm. The white American equations gave a stature of 1,720 mm for the female and a mean of 1,750 mm for the three males. This lesser mean still marks them as a tall group. However, the much tighter range of estimates from the three arm bones of individual 6 using the Polynesian equations suggest that these more accurately mirror the body proportions of the individual, and thus are more appropriate for stature estimate. A similar pattern is suggested with the other

Table 3. Mandibular measurements in millimetres of individuals 3 and 6; definitions follow Morant (1936).

Individual	3	6
bicondylar breadth	141	120
bigonial breadth	109	98
condylar length	–	24
ramal breadth	43	45
ramal height	60	72
symphyseal height	35	31
body height	33	29
body length	106	100
mandibular angle	112	95

individuals, where the radius of individual 2 gives a higher stature estimate with the white American equation than with the Polynesian; and the humerus of individual 5 gives a higher estimate with the Polynesian equation.

Two male second metacarpals were X-rayed for cortical structure. These gave standardised thicknesses (Nordin's score; Barnett & Nordin, 1961) of 52.5 and 51.0.

Dentition. The material was limited to the near-complete dentitions of individuals 3 and 6, and two isolated teeth.

(a) morphology. The recorded features are set out in Table 5, together with dental pathology.

(b) metric data for individuals 3 and 6 are given in Table 6.

Pathology. *(a) Skeletal*. Two lesions were identified. (i) A lesion was present in the upper shaft of the left femur of individual 6 (Fig.4). The appearance of this suggests a periostitis, a localised and essentially superficial bone infection secondary to an overlying soft tissue lesion. Radiology supports this diagnosis, showing minimal involvement of the deeper cortex and no encroachment on the medullary cavity. Neither in appearance nor site does this lesion suggest yaws.

(ii) A proximal hand phalanx from individual 3 showed expansion of the proximal end and pathological antero-posterior bowing of the whole shaft (Fig.5). Radiology showed a rather thin structure to the proximal expansion, but some thickening of the involved distal cortex. The general appearance is suggestive of a chronic granulomatous infection, of which yaws is a possibility.

(b) Dental (Table 5). Pathology here was limited to a moderate degree of alveolar erosion in individual 3 and a rather lesser degree in individual 6. The assumption is that the overlying pathology was periodontal disease. There was no enamel hypoplasia, caries, advanced attrition, or staining suggestive of betel chewing.

Distance analyses. Penrose Size and Shape statistic was applied to mandibular metric data, utilising five and seven dimensions and comparative data from other

Table 4. Stature in millimetres, derived from White American equations (Trotter, 1970) and Polynesian equations (Houghton *et al.*, 1975). Long bone lengths are given; see text for further comment.

Individual	White American	Polynesian	Bone length
2 (female)	1720	1659	right radius 247
3 (male)	1750	1798	right femur 477 (est)
5 (male)	1720	1753	left humerus 331
	1715	1767	right fibula 372(est)
6 (male)	1780	1800	left humerus 350
	1860	1809	left ulna 307
	1875	1805	both radii 285
Male mean	1750	1784	

Table 5. Dental morphology and pathology.

Individual		3	6
shovel-shaped	I1	nil	nil
incisors	I2	nil	trace
maxillary molar	M 1	D4	D4
crown morphology	M 2	D4	D4-
	M 3	?	D3
Carabelli cusp		nil	nil
mandibular molar	M 1	?5	?4
crown morphology	M 2	+5	+4
	M 3	+4	+5
protostylid		nil	nil
third molars	All erupted in both individuals, but 28 and 38 hypoplastic in Individual 3.		
calculus		slight	slight
alveolar erosion		moderate	slight
caries		nil	nil
enamel hypoplasia		nil	nil

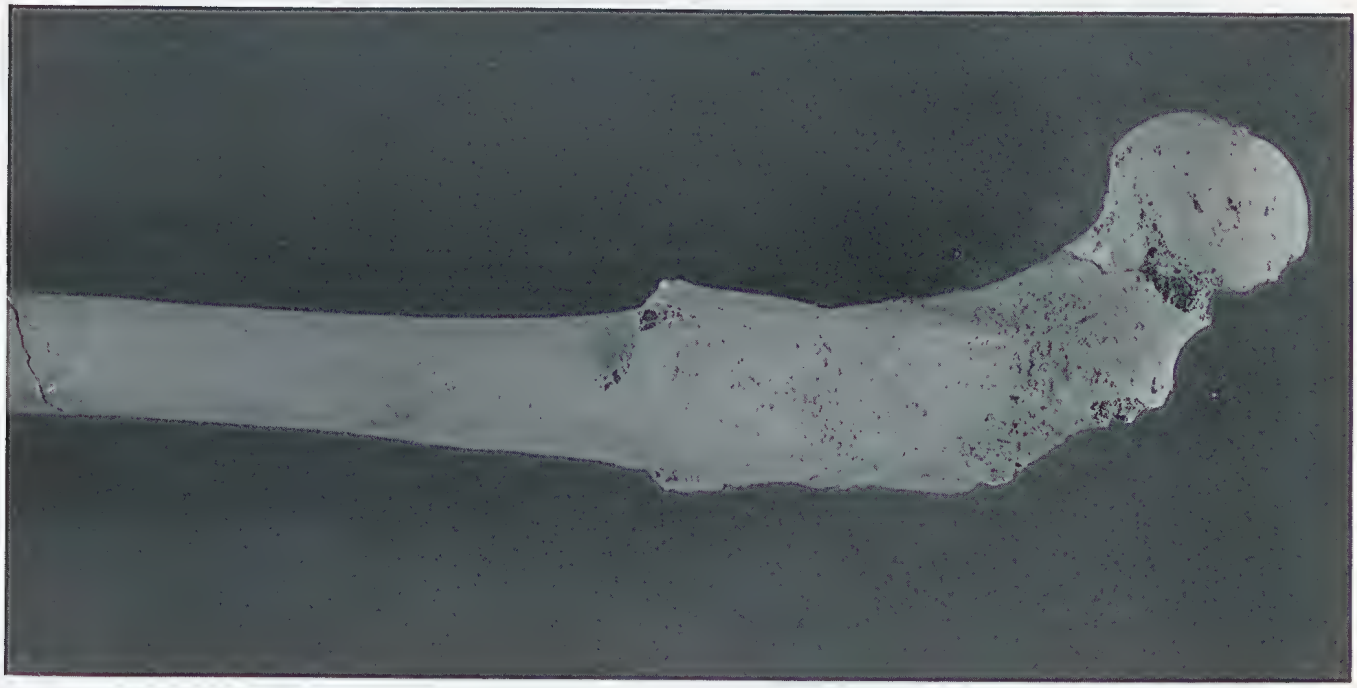

Fig.4. Proximal end of left femur, The thickening of the upper shaft is superficial and probably secondary to overlying soft-tissue infection.

Table 6. Watom tooth dimensions in millimetres; the FDI classification is used.

Maxillary

Individual	Quadrant 1							
	11	12	13	14	15	16	17	18
	length							
3	9.5	8.1	8.8	8.0	7.3	11.6	11.4	
6	9.1	7.2	8.0	6.4	6.2	10.0		8.2
	breadth							
3	7.8	7.2	8.8	10.1	9.2	12.1	12.6	
6	7.8	6.4	8.5	9.9	9.9	12.2		11.3
	Quadrant 2							
	21	22	23	24	25	26	27	28
	length							
6	9.0	7.2	7.9	6.5	6.0	10.0	9.5	8.0
	breadth							
6	7.4	6.7	8.5	10.0	9.9	12.2	12.0	10.7

Mandibular

Individual	Quadrant 3							
	31	32	33	34	35	36	37	38
	length							
3	5.8				8.5	12.5	12.5	12.2
6	5.2	6.2	6.7	6.5	6.7	10.7	10.5	11.3
	breadth							
3	6.0				9.7	11.8	11.9	10.7
6	5.7	6.1	8.2	7.8	8.0	10.5	10.0	9.9
	Quadrant 4							
	41	42	43	44	45	46	47	48
	length							
3			6.4	7.8	8.9	12.7	13.0	12.2
6	5.3	6.2	6.8	6.2	6.5	10.7	10.3	11.0
	breadth							
3			8.0	8.5	9.2	11.8	11.0	10.0
6	5.7	6.2	8.0	7.9	8.0	10.3	10.0	9.8

Fig.5. Proximal hand phalanx of individual 3 showing a chronic granulomatous reaction with expansion of the proximal end and ventral bowing of the shaft.

populations. The results are set out in Tables 7 and 8, and graphically for the five-dimensional analysis in Fig.6.

Table 7. Penrose analysis on seven mandibular measurements.

Group	Size	Shape	C.R.L
Watom	0.00	0.00	0.00
New Zealand	0.02	1.68	1.70
Hawaii	0.00	1.93	1.93
Namu	0.19	1.76	1.95
Tonga	0.04	2.13	2.17
Africa	0.53	3.50	4.03
Sarawak	0.61	4.14	4.75

Table 8. Penrose analysis on five mandibular measurements

Group	Size	Shape	C.R.L.
Watom	0.00	0.00	0.00
New Zealand	0.20	1.12	1.32
Hawaii	0.55	0.82	1.37
Tonga	0.96	0.62	1.58
Namu	1.22	0.87	2.09
New Britain	1.23	0.87	2.10
Vanuatu	2.34	0.79	3.12
Africa	2.93	1.28	4.20
Nebira	3.31	0.93	4.24
Sarawak	3.68	0.79	4.47

A similar analysis was carried out on the dentition. These results are given in Table 9 and Fig.7.

Discussion

Health and biological affinities are discussed.

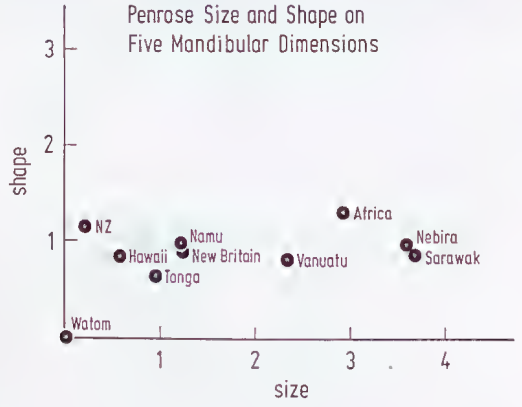

Fig.6. Penrose Size and Shape analysis on five mandibular dimensions from Watom Individuals 3 and 6. The comparative groups are described in Appendix B. HPNG = Highland Papua New Guinea.

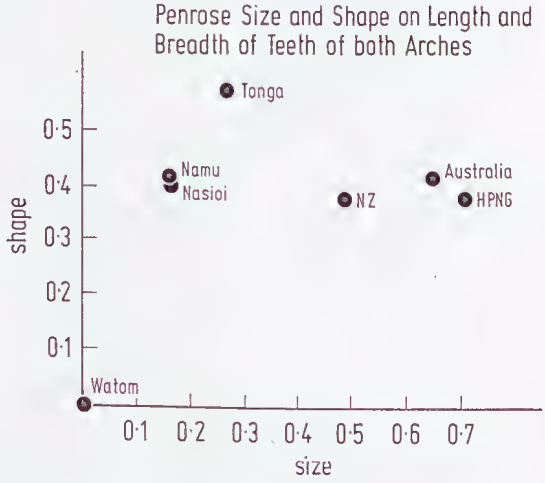

Fig.7. Penrose Size and Shape analysis on tooth dimensions of individuals 3 and 6. The comparative groups are described in Appendix C. HPNG = Highland Papua New Guinea. NZ = New Zealand.

Table 9. Penrose analysis of tooth dimensions.

Group	Size	Shape	C.R.L.
Watom	0.00	0.00	0.00
Nasioi	0.16	0.40	0.56
Namu	0.15	0.42	0.57
Tonga	0.27	0.58	0.85
Maori	0.49	0.38	0.87
Australian	0.65	0.42	1.07
PNG	0.71	0.38	1.09

Health. The mean age at death of the adults is unremarkable for prehistory and with the unreliability inherent in this small and fragmented series allows no conclusions to be drawn. The stature data indicate not only a genetic potential for tallness (see below), but also a reasonable diet and general environment during the growth period. The rather low Nordin's score on two individuals does suggest that stature was achieved somewhat at the expense of bone robusticity and that at times during the growth period there might have been some dietary inadequacy. Recent well-nourished groups give a Nordin's score in the 57–63 range; prehistoric Namu is 57 and prehistoric New Zealand 53 (Houghton, 1980). The teeth show no transverse lines or other enamel hypoplasia. The general conclusion is that these people lived in a fairly favourable environment. It is possible that yaws existed amongst them.

Biological affinities. In view of the significance of Lapita ware in current theories of Pacific settlement and Polynesian origins, preliminary comment is necessary on the model used here regarding human relationships within the Pacific, and the settlement of Polynesia. In tersest form the model states that the dominant settlement of Polynesia was from Island Melanesia, by a group that was part of the human population of that geographic region; that is, they were not in transit through Melanesia from more distant parts. This model was originally adopted as appearing biologically valid and being the most parsimonious of the possibilities. Polynesians, considering their wide geographic distribution, show a remarkable biological homogeneity (Houghton, 1980). This homogeneity strongly suggests origin from a rather small founding group. Melanesians, by contrast, in terms of both body morphology and the numerous tissue polymorphisms that now are measurable, show great biological diversity. Indeed the term melanesian is a geographical statement, being someone living within Melanesia; it cannot be a fairly closely-defined biological statement as can the term 'Polynesian'. To settle Polynesia with a group evolved from one of the varied populations of Island Melanesia makes the simplest plausible thesis, requiring least voyaging (though the distances are formidable enough) and no long transits through (purportedly) genetically alien territory. Recently this model has been supported by two very different forms of analysis. Firstly, gene mapping is now starting to reveal some unique relationships between human groups in Melanesia and Polynesia (e.g. Hill *et al.*, 1985, 1987; Trent *et al.*, 1985). Secondly, the distinctive Polynesian morphology has been demonstrated to be a crucial selective adaptation to the particular conditions of the oceanic environment, and an inappropriate form for the environment further west (Houghton, in press). The latter study demontrates that the Polynesian body form evolved within the Pacific.

This model may be contrasted with the lingering view that "...as physical human beings, the Polynesians simply could not have emerged from any eastern Melanesian population; they are just too different genetically. Skulls and the living agree" (Howells, 1973: 234). The gene mapping results dispose of this argument *vis-a-vis* the living. Regarding skulls, much craniological data used in distance studies has been obtained from museum collections of indeterminate temporal provenance, but in general dating to late prehistory or the protohistoric period. Yet the time dimension is actually crucial, and it simply is not valid to compare data from ill-defined collections of recent crania from widely separated parts of the Pacific and its rim, and claim biological significance for the results. Indeed, in these studies biological justification for the measurements used is usually entirely lacking. On the statistical side, very small samples and incomplete matrices often violate the premises on which multivariate statistical theory rests. For valid comparison, adequate samples from well excavated and dated sites from prehistory are needed. Fortunately these are starting to emerge; e.g. Davidson & Leach (in preparation), Best (1987). In the meantime, the comparative groups used here fall far short of the ideal, but in Appendices B and C they are described, and their selection and the measures used are justified as far as possible. There may be other suitable comparative groups of which I am unaware.

The model used here is examinable against data from relevant groups. It is desirable to have a model, for the inexorable (and often contradictory) outpourings of data and dendrograms that emerge from the fusion of craniometric data, multivariate statistics and computer power, have the potential to illustrate inductive method at its worst.

Comment is also necessary on the statistics, here confined to the use of Penrose's Size and Shape, a refinement of Pearson's original Coefficient of Racial Likeness (CRL). The CRL has had a bad press, and regularly is dismissed as inadequate because it does not allow for correlation between variables. For that reason, the Mahalanobis D^2 has swept the field. Yet the concept of functionally-significant uncorrelated variables within a biological structure is a difficult one, which its proponents need to explain. Anyway, the use of CRL or one of its derivatives receives support from a statistician:

> D^2 differs fundamentally from the other two distance measures because it eliminates redundant variables and the others do not....Both DD and CRL increase when adding a variate that is completely correlated with those already included, but D^2 remains unaltered. Now it seems to me that the human mind distinguishes between different groups or populations *because* there are correlated characteristics within the postulated groups.

To quantify this idea, some measure of distance such as DD or CRL is necessary; D^2 will not do, because of the way it eliminates correlations. When populations have been established, D^2 becomes useful and is essential when building up discriminant functions. These two aspects of distance must be distinguished and carefully considered.....(Gower, 1972).

In turn, it seems to me that this has been one of the problems in using osteometric data in distance studies. Groups from different sites or regions have been considered to be biologically distinct, whereas the first statement can only be that they are geographically distinct. For initial analysis, CRL or its Penrose elaboration seems most appropriate. It is also my feeling that progress in this difficult field depends on a deeper analysis of the biology of the particular situation, rather than increasing refinement of statistical method. Statistical analyses properly belong as addenda to quite complex biological considerations. The biological validity of the data are all-important, and no amount of manipulation of irrelevant data will produce anything of worth (see Rhoads (1984) for more on this theme).

With that background, and in the light of the biological model set out above, comment is possible on the results. The large body build dominates the findings. While the limitations of the sample must be continually born in mind, the mean male stature of 1784 mm is exceptionally tall for a prehistoric group, and the female also is tall. The tallest individual has rather gracile infra-cranial bones relative to the others, but all show bony evidence of a well-developed musculature. This large body phenotype, inappropriate to the land-dominated tropical environment to the west, places the Watom people firmly with other large-bodied ocean voyagers and small-island dwellers, whose most evident living representatives are the Polynesians.

The mandibular analysis using five dimensions (which each express some major structural and functional component) gives closest relationship with two eastern Polynesian groups, then Tonga, and Namu. The dental analysis places Namu practically as close as the recent Melanesian Nasioi, with Tonga and New Zealand a little further away. Care is particularly needed in interpreting these dental data, or indeed any craniofacial data, for they are profoundly influenced by total body form and environment (Houghton & Kean, 1987). The changing biomechanics of the mandible with changing body size contributes to a negative allometric relationship with the dentition; that is, teeth get relatively smaller with increase in overall body size. Thus, although individuals may show teeth of rather similar dimensions it does not follow that close biological affinities are indicated; similarity in size between teeth of large and small-bodied individuals may reside not in some specific and autonomous genetic control of tooth size common to both groups, but may be a metric coincidence reached through different influences. With these caveats, it may be said that together, these analyses support the thesis of affinities both with groups now regarded as Polynesian or having Polynesian associations (Namu), and with recent Island Melanesian groups.

The chord measurements obtained from the vault bones of individual 6 merit comment. It is known that the proportions of the three major vault bones differ between different parts of Oceania; for example Polynesians tend to have a rather long frontal bone whereas some groups from New Guinea show an opposing tendency (Wagner, 1937). The biological basis of these differences is still uncertain. It may relate to underlying cranial base morphology. More probably it simply reflects overall head length, the parietal bone contribution dominating as the vault elongates. The Watom fronto-parietal index of 100.00 falls between the recent Polynesian values of around 96–97, and recent values from Island Melanesia of around 105–106. The parieto-occipital index of 82.2 is very low, and may contain some element of distortion of the bones. The Polynesia value for this ratio usually lies in the 93–94 region, and those from geographic Melanesia in the high eighties. However, the only values lower than 82 recorded by Wagner (1937) are in two small series from Fiji and Vanuatu, suggesting an eastern Melanesia/western Polynesia affinity. But despite the space spent on these cranial dimensions it should be appreciated that the weightier conclusions derive from the stature data, and the mandibular and dental analyses.

My conclusion is that the morphology of the Watom people is fully compatible with that to be expected, on biological grounds, of oceanic voyagers and small-island dwellers, and thus of the earliest settlers of western Polynesia. While synthesis of biological and cultural (and linguistic) findings must always proceed with great caution, claims that the Polynesians derive from the creators of the Lapita culture of the western Pacific are supported by this analysis of the human material from the Reber-Rakival site. From this body form, within Polynesia successive episodes of genetic drift would readily have allowed the more extreme eastern Polynesian morphology to be derived. This body form of course remained totally appropriate to the oceanic environment.

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Appendix A. Census

Individual 1.
Age: mature adult
Sex: female
Material: scanty and fragmented. No skull. A solitary left maxillary canine, but this cannot be assigned to the person with certainty. Fragments of most upper limb bones. Atlas and axis, and bodies of three other cervical vertebrae; fragments of lower vertebrae. Pelvic fragments and upper 60% of right femur. Several foot bones, especially tarsals.

Individual 2.
Age: mature adult
Sex: female
Material: no skull or teeth. An almost intact right radius, lacking only the styloid process (estimated maximum length 247 mm); otherwise material is limited to fragments of forearm bones, tibiae and femora, and a few pieces of vertebrae.
Comment: When estimating stature, 10 mm was added to the measured length of right radius to allow for the missing styloid process.

Individual 3.
Age: 25–30 years
Sex: male
Material: crushed and distorted cranium. Largely intact (reconstructed) mandible. Nineteen teeth present. Some scapula and humeral fragments. Three intact cervical vertebrae and fragments of lower vertebrae. Pelvic fragments. Right femur missing only upper end (estimated maximum length 477 mm), and shaft fragments of all other major leg bones. Some foot bones.
Pathology: there is moderate erosion of the alveolar bone of both jaws. A proximal hand phalanx shows involvement by some chronic granulomatous condition, with expansion of the proximal end and general bending of the shaft; the gross and X-ray appearance is compatible with but not diagnostic of yaws.
Comment: I retain a residual suspicion that this individual could be female. This is based on the rather equivocal pre-auricular grooves of the pelvis, and on the small cranial measurements. If female, she is particularly tall and robust, and the general comments on stature for the group are reinforced. Nordin's score for the second metacarpal is 52.5.

Individual 4.
Age: 30+ years
Sex: male
Material: there are fragments of vertebrae, clavicle,

humerus, pelvis, femur, and a few hand and foot bones. Overall representation is minimal. An upper left third molar cannot with certainty be assigned to this person. In addition there are upper limb fragments of a more gracile individual, probably female.

Individual 5.
Age: 30+ years
Sex: male
Material: complete left humerus of maximum length 331mm; shaft of right humerus; left clavicular fragment; scanty fragments of all vertebral regions; pelvic fragments; almost intact right fibula, of estimated maximum length 372mm; some hand and foot bones.

Individual 6.
Age: mature adult
Sex: male
Material: skull, malars and supraorbital margin, substantial left temporo-parietal fragment, and many lesser pieces; largely complete (reconstructed) mandible; complete dentition except for right maxillary second molar; intact left humerus (350 mm), left ulna (307 mm) and both radii (both 285 mm), with fragmentary representation of all other upper limb bones. Radio-humeral ratio of 0.81. Hip fragments, and largely complete femora and tibiae, though insufficient for stature estimates. Some fibula fragments, and foot bones.
Pathology: there is a lesion of the upper shaft of the left femur, probably a periostitis secondary to overlying soft tissue infection; this is not typical of yaws, though this aetiology cannot be excluded.
Comment: despite (or because of) the stature, the long bones of this individual are rather gracile. The Nordin's score of 51 is rather low in comparison with contemporary well-nourished groups who have values above 57.

Individual 7.
Age: mature adult
Sex: male
Material: this is minimal; a right femoral shaft, otherwise wide but very scanty and fragmented skeletal representation.

Individual 8.
Age: 25+ years
Sex: male
Material: minimal, the main representation being shaft fragments of both tibiae and fibulae, and many foot bones.
Comment: although close to individual 1 excavated in 1965, these are clearly different people.

Child.
Age: two years.
Material: cranial fragments; an incisor that cannot certainly be assigned to this individual; shaft fragments of all upper limb long bones; rib fragments; complete left tibial diaphysis (155 mm) and left femoral diaphysis, with some epiphyseal fragments of the latter.
Comment: this individual was contained under 'miscellaneous bones' and seems not to have been identified at excavation. It may not belong to SAC locality (see Green, Anson & Specht, this volume).

Rectangle IV material.
A small and chaotic amount of largely adult material that I can neither fit with the discrete individuals nor sensibly relate within the rectangle. Fragments of two adult mandibles are present.

Appendix B. The mandibular comparative material.

(i) Measurements. The definitions are those of the Biometric School (Morant, 1936). The seven used here I consider to express some basic functional parameters. The bicondylar width gives a guide to the width of the cranial base, a fundamental skull template. The bigonial width contains some of the same information and also an indication of lower facial width. Ramal breadth particularly relates to the degree of development of the masticatory muscles, while ramal height gives an idea of the height of the nasal airway (and thus overall body size) and is also influenced by cranial base angle, another fundamental base parameter. Mandibular angle contains much the same elements of information as ramal height. Mandibular length gives an idea of the overall anterior projection of the facial skeleton. Symphyseal height gives an indication of the height of the basal component of the bone anteriorly (the alveolar contribution is fairly constant between groups) and this in turn is related to the pattern of growth of the bone, with relationships to such measurements as mandibular angle and ramal height.

(ii) Comparative series. Included here is comment on the environment of the group (which strongly influences phenotype) and the justification for using the group in the analysis.

Namu. A series of 13 drawn from material excavated by B.F. Leach and J. Davidson in 1977 on Taumako, a Polynesian outlier of the southern Solomons. The material is dated to about A.D.1200–1400. Although this group suffered severely from yaws, nutrition was good during their developmental years, with development of a robust body form (Houghton, unpublished report). The series was used as an example of an eastern Melanesian (in geographic terms) morphology.

Hawaii. A series of 125 (Snow, 1974) from Mokapu, probably dating to the late prehistoric. Included as an example of eastern Polynesian morphology.

Nebira. A series of 10 individuals from a lowland New Guinea site, some 20 km inland from Port Moresby, dated to about A.D.1500 (Bulmer, 1979). These are small, gracile people who were almost certainly existing in a region of endemic malaria. Their mandibular phenotype will have been influenced by this poor environment. Included to represent a New Guinea group from prehistory. Adequate representation by one group of course is unrealistic, and the environmental conditions make it a poor

example; but I could find no other discrete group. The placing of this group in the analysis is probably most uncertain.

New Zealand. Unpublished data from 126 individuals, measured by the author. The material is drawn from the whole country, and largely belongs to the late prehistoric – say A.D.1600–1800. The limited gene pool that seems to be represented in the New Zealand skeletal phenotype justifies the use of a group with fairly wide geographic spread. In general, nutrition was fairly good for these people. Like Hawaii, the group was chosen to represent eastern Polynesian morphology, with the hope that the analysis would place the two groups fairly close together.

Tonga. Data on 16 individuals, largely from material excavated at 'Atele (Davidson, 1969), and dated to about A.D.1200. These were generally robust, healthy people. Used as an example of western Polynesian morphology from prehistory.

Sarawak. These data are on a series of 12 from Mulu cave (Hughes, 1963). Their date in prehistory is uncertain, but the series was used to provide some representation from that region. There is no information on the health of the group.

Africa. These data are from a recent series of 488 individuals from South Africa (de Villiers, 1968), and were introduced to test the ability of the statistical method to distinguish such an exotic group. There is no information on the health of the group.

Appendix C. The dental comparative material.

Namu. See under Appendix A. The dental data are from 70 individuals, measured by the author.

New Zealand. See under Appendix A. The dental data are on 30 individuals.

Tonga. A very small series of four individuals from the late prehistoric period (Anderson, 1978). Bone robusticity suggests that nutrition and environment were good. Unpublished data by the author.

Highland Papua New Guinea. Data obtained from casts on a series of 32 contemporary males from Goroka in the eastern Highlands region (Doran & Freedman, 1974). I have no information on nutrition and environment, although the authors comment that the group were 'in close contact with urbanization'. The group was used to provide comparative data from the region, but the contemporary nature of the material is a disadvantage.

Nasioi. Contemporary data from casts of 60 individuals of the Nasioi people on Bougainville (Bailit *et al.* 1968). Nutritional and environmental status unknown. Again, the dating is a disadvantage.

Australian. Data from casts of 41 individuals of the Wailbri (Walpiri) tribe, living 'under settlement conditions' at Yuendumu, South Australia (Barrett *et al.* 1963, 1964). Casts taken between 1950 and 1960. Environment and nutrition unstated but probably not very good. This group was introduced to provide a recognised extreme in size of dentition.

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A Study of Skeletal and Dental Remains from Watom Island and Comparisons with Other Lapita People

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ABSTRACT. Human skeletal and dental remains from Watom Island, East New Britain Province, Papua New Guinea, dated circa 500 to 100 years BC and associated with the Lapita cultural complex are described. The remains, often poorly preserved and incomplete, include six adult male and two adult female skeletons. Morphometric features of the mandible include a broad short mandibular body, divergent ramus and the rocker jaw condition. The teeth, slightly to moderately worn, are small, caries free and exhibit periodontal disease. Males are tall (174 cm) and the long limb bones are typically gracile. Squatting facets and costo-clavicular sulci are common. Except for a few, mostly minor, healed bone fractures, there is little evidence of disease. Comparisons indicate that the people of Watom are, in some respects, similar to Polynesians and other Pacific populations by virtue of their tall statures, rocker jaws and shovel-shaped incisors but they further exhibit striking morphological differences, such as small teeth, gracile long limb bones and broad short mandibles not seen in other Pacific populations. Multivariate analyses of mandibular measurements reiterate this unique Watom mandibular morphology and further separate the Watom and Lapita samples from Polynesian samples. Broader multivariate comparisons place Polynesians with South-east Asian and East Asian groups well differentiated from Melanesian samples lending support to the view that Polynesians are not of Melanesian origin. A weaker connection between Lapita Watom people and mandibular samples from eastern Melanesia and Polynesia is further implied in these results. Finally, this study demonstrates that until larger and earlier dated Lapita skeletal remains become available, the biological relationships and origins of the Watom and Lapita people remain elusive.

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Human remains associated with the Lapita cultural complex (ca. 3,600 to 2,500 YBP), are extremely rare. Lapita skeletal remains are a prerequisite for understanding the biological origins of the Austronesian-speaking populations of eastern Melanesia, Polynesia and central Micronesia. Site SAC (Site 8) in Rakival Village on Watom Island, East New Britain Province, Papua New Guinea, although relatively late in the Lapita sequence (ca. 500 to 100 BC), has provided more human remains than all other known Lapita sites combined. Thus far the remains of at least eight individuals are represented in the Watom Island sample.

The following account summarises the results of an osteological-odontological study of the Watom Lapita remains. The initial examination of these remains was made by Pietrusewsky over a six week period in mid-1987 at the Department of Anatomy, University of Otago in Dunedin, New Zealand. The sections include methods and material, individual descriptions of the burials, a summary of the metric and non-metric observations recorded in the skull, teeth, and infracranial remains, evidence of disease and the general state of health of the Watom individuals. Univariate and multivariate comparisons with other Lapita remains and more modern populations from the Pacific and surrounding regions conclude the report.

Appendix A includes all plates and Appendix B includes all tables referred to in the text.

Material and Methods

Watom burials. In 1966, Jim Specht excavated three human skeletons from Trench I (later renamed Rectangle I) in Locality SAC (originally coded as Site 8 or FAC) at the Reber-Rakival site on Watom Island (Specht, 1968). In 1985, as part of the Lapita Homeland Project, Roger Green and Dimitri Anson excavated five additional skeletons from Rectangles I, II and IV at the same site. All burials, which are from the basal grey sand midden layer, are dated circa 500 to 100 BC, probably toward the latter end of that range (Green & Anson, 1987). The burials, which occur mostly in pits, were in extended and flexed positions. Most of the skeletons were missing their skulls. Because of their repeated exposure to the high tide water level, the remains were found to be in a generally deplorable condition at the time of their excavation (Green, personal communication).

Laboratory procedures. All skeletal remains from Watom, including those excavated by Specht in 1966, were examined by Dr Philip Houghton of the University of Otago prior to the present study. While most of the material had been unpacked before the present study was initiated, there were some exceptions. For example, a small box associated with Burial 2 which bore the inscription "metacarpals, metatarsals and phalanges", appeared not to have been opened. Each bone was found to be individually wrapped in tissue (waxed) paper. Careful inspection of this material, resulted in identification of not only metapodial and phalanges but the distal ends of the right fibula and ulna. Further, there were a great many smaller bags containing isolated teeth and fragments of bone and other non-human remains (i.e. sand, shell, coral, cultural and faunal remains) not directly associated with any of the major burials. This latter (miscellaneous) material, which was boxed separately by the excavators, had received little attention prior to the present study.

While some reconstruction (mending of the broken mandibles and some of the other limb bones) had been attempted previously, a large portion of the remains had not been sorted or cleaned. Before any data were recorded, the remains were first washed (using cold water) to remove the dirt and encrustations which covered most of this material. Mechanical means were used to remove the latter deposits. Sorting and identification of the remains were then initiated. Using a water soluble glue, some of the broken bones were mended. The miscellaneous remains were subjected to the same treatment. Using the provenance information written on the outside of the bags containing the scattered remains and the excavator's fieldnotes and excavation grid, much of the miscellaneous material could be assigned to one of the major burials. The material which was added to the major burials is documented in Appendix A which further contains a complete inventory of all miscellaneous remains.

Once the remains had been cleaned, mended and identified, an inventory of the completeness of each burial was made by coloring in the appropriate areas of standard skull and burial register forms used at the University of Hawaii. These and other forms used in the present study are available, upon request, from the author. Metric and non-metric observations were recorded in all skeletal and dental remains using additional standard forms. These completed forms are kept on file in the Department of Anthropology at the University of Hawaii, Honolulu.

Other Lapita remains or remains contemporaneous with Lapita. Other known Lapita skeletal remains, or those which are contemporaneous with the Lapita cultural complex, used in the present study for comparison with the Watom material include:

1. Lakeba, Fiji. The fragmentary remains of at least two

individuals from Lakeba, a Lapita site in the Lau Group, Fijian Islands, were excavated by Simon Best (1977). The site's initial occupation dates to the early part of the first millennium BC and the burials are from the middle part of that interval. This material was examined and described by Houghton before it was returned to Lakeba for reburial (see Houghton, this volume). Observations used in the present study were recorded by the author in 1983 on two mandibles [one is a cast (Lakeba 1) and the other is an original specimen (Lakeba 2)].

2. Natunuku, Fiji. This is a partially complete skeleton of an adult male excavated by Elizabeth Shaw (1967, 1975) at Natunuku VL1/1, an early Lapita site on Viti Levu of the Fijian Islands which has a date of 1,590 ± 100 yr BC, although others (Green, personal communication; Spriggs, personal communication) argue that, while early in the Fijian Lapita sequence, the burial is probably not as early as the 1,500 BC date often assigned to it. Previous attention has focused almost exclusively on the mandible, the most complete bone in these remains (Pietrusewsky, 1985a, 1985b). A more complete description of the Natunuku skeleton appears in this volume.

3. Tonga. Skeletal remains, originally designated Burial AK by Poulsen (1987:21), are from Burial Pit AF of Trench III at site To.1, a Lapita site located in Pea township, Tongatapu, Tonga. While Spennemann (1987) has concluded that at least three individuals are represented, this investigator, after examining the same material in 1987 at the Department of Anatomy, University of Otago, agrees with Houghton's assessment that the mandible belongs to the main burial. Other intrusive remains (e.g., a left third cuneiform, fragment of proximal end of a left ulna and distal third of a left humerus) represent at least one additional individual (see Houghton, this volume). Plates 29 and 30 exhibit some of the bones from this burial.

4. Manus. A mandible fragment excavated by W. Ambrose in 1981 from a site in Baun Village on Lou Island, Manus Province, Papua New Guinea. The dates for the site have been recently revised to circa 2,100 YBP (Ambrose, 1988a, 1988b). While the pottery and other aspects of the archaeological record found in association with the Manus mandible are not Lapita, the mandible is contemporaneous with the latest phases of the Lapita culture further east. The mandible was examined by the author during a brief visit to the Australian National University in Canberra in 1987.

Age determination. Standard osteological and forensic criteria were used to determine the age-at-death (Anderson, 1969; Bass, 1988; Brothwell, 1981; El-Najjar & McWilliams 1978; Krogman & Iscan, 1986; Stewart, 1979; Ubelaker, 1984). Among the methods used were epiphyseal union, tooth calcification and eruption, metamorphosis of the symphysis pubic bone (McKern & Stewart, 1957; Gilbert & McKern, 1973) and cranial suture closure. Given the fragmentary nature of the Watom remains, determining the exact age for adults was generally compromised. Degenerative changes in the limb bones and vertebral column and tooth wear provide more general impressions of age, which are used to augment estimates based on the more reliable methods of age determination.

Sex determination. The morphological appearance of the pelvis (e.g. sciatic notch, ventral arc, subpubic angle, pelvic shape, etc.), cranial indicators and limb bone diameters were found to be the best criteria for determining the sex of adults.

Measurements. All measurements, recorded to the nearest millimetre, follow standard osteometric techniques (Martin, 1957; Howells, 1973). Swiss-made sliding, spreading and small coordinate calipers, a mandibulometer and an osteometric board were used to record these measurements. Tooth measurements (recorded to the nearest tenth of a millimetre) were made using a dial Helios caliper fitted with pointed tips.

Following standard convention, measurements were recorded on the left side in the skull. If the left side was not present, the same measurement was recorded on the opposite side. Measurements were recorded on both sides in the infracranial skeleton.

Stature estimation. Estimations of stature are based on formulae of Trotter (1970) and Houghton *et al.* (1975). The latter have a tendency to give slightly taller stature estimates. In a few instances, when the limb bones were not complete, the maximum lengths were estimated from one of the several segment measurements using the method described by Steele (1970).

Non-metric observations. Observations of non-measurable morphological features (e.g. metopic suture, squatting facets, rocker jaw, etc.) follow the work of several investigators (e.g. Pietrusewsky, 1969, 1974, 1976; Brothwell, 1981; El-Najjar & McWilliams, 1978; Saunders, 1978).

Pathology. Observations of diseased bone are presented in the individual burial descriptions found in Table 1. Observations of dental pathology, including tooth loss, periodontal disease, caries, enamel hypoplasia and dental wear are summarised in the section on teeth. Degenerative changes in the infracranial skeleton and vertebral column were systematically scored for each articular surface using the scale: absent (0), slight (+), medium (++) and marked (+++) depicting the degree of osteoarthritic lipping. All observations of pathology were restricted to the macroscopic level of inspection.

Statistical analysis. All data were analysed using the IBM 3081 mainframe computer at the University of Hawaii-Manoa computing center. Various statistical packages, e.g. SAS-Statistical Analysis System, BMDP (Dixon & Brown, 1979) and other specially written computer programs were utilised in analysing the data. Both univariate, (descriptive statistics) and multivariate procedures (e.g. Mahalanobis' Generalized Distance, stepwise discriminant function analysis and regression analysis) were employed. All data are currently stored on magnetic tapes at the University of Hawaii.

Burials

The Watom burials exhibit considerable postmortem damage as a result of natural disturbances and exposure to periodic high tide water levels. General preservation of these remains ranges from poor to fair. Burial 6 is the best preserved skeleton. Although the cranium of the latter is mostly missing and fragmentary, the rest of the skeleton is relatively complete and includes several intact upper limb bones. With the exception of hand and foot bones, the bones of the remaining Watom burials are frequently incomplete.

Six of the eight Watom burials are missing skulls. Two of the former burials possess upper cervical vertebrae suggesting that the heads had not been removed prior to or around the time of burial and that natural disturbances probably account for their absence. The crania of Watom Burial 3 and 6 are very incomplete and poorly preserved. Four mandibles, none perfectly preserved, were identified in these remains. Two of the latter belong to major burials and two (M1 and M2) were identified in the miscellaneous remains from the site.

Two females are represented in the remains from Watom, one between 18 and 20 years of age and the second approximately 30 years of age at time-of-death. The remaining skeletons are adult males who range in age between 30 and 35 years. There are no subadults or individuals of old age.

Table 1 summarises some of the salient features recorded for each burial. The features include the burial's provenance, age-at-death, sex, stature, completeness, preservation, pathology/anomalies and other comments.

Skull

Only two skeletons are represented by cranial remains, Burials 3 and 6 (Plates 1-11). For each, the mandible is the best preserved bone. The warped cranial vault remains from Burial 6 include the left temporal and a portion of the parietal bone. Other identifiable vault bones from this burial include two substantially complete zygoma bones and the left maxilla. The rest of the cranium is represented by numerous vault fragments. Large areas of the face and base of the skull are missing. Reconstruction of these remains is limited.

The skull of Burial 3 is more complete but not intact. The frontal, right (warped) parietal and right zygoma are substantially complete and disarticulated. Most of the left parietal, both temporals and the occipital bone are further preserved. The cranial vault bones form a calcified mass which prevents reconstruction. Alveolar prognathism is observed in the remains of this individual.

Measurements recorded in the two crania (Table 2) and four mandibles, all adult male, are presented in Tables 2 and 3 respectively. A summary of the means and standard deviations of these mandibular measurements and indices are presented in Table 4. This table further presents measurements recorded in the Lakeba and Natunuku mandibles.

Two conspicuous features observed in the Watom mandibles are the short body lengths and wide ascending rami. The mandibular index, which measures the length of the mandible relative to the breadth, confirms this visual appraisal. The ramus index (N=3) further indicates the ramus has a very broad shape. The uniqueness of the Watom mandibles will be addressed later. A summary of the non-metric variation recorded in the Watom and other Lapita-associated crania and mandibles are presented in Tables 5 and 6.

The Watom mandibles uniformally exhibit single mental and mandibular foramina and further lack mandibular tori and bridging of the mylo-hyoid groove. Complete or partial rocker jaw was recorded in three of the four mandibles from Watom. The shape of the chin is pointed medially and is frequently associated with a slight inferior angulation at the symphysis menti in two of the four Watom mandibles examined.

Teeth

Tooth measurements. Mesial-distal and buccal-lingual crown diameters and cross-sectional areas were recorded in the permanent teeth of three individuals from Watom. Summary statistics of these measurements recorded in the Watom teeth and several other Lapita samples are given in Table 7. Using the mean cross-sectional areas for each dental tooth category (sexes and sides combined), a tooth summary figure of 1140 was calculated for the Watom sample. While sample size is small (N ranges from 2 to 4), this figure confirms the general impression that the Watom teeth are small. Comparisons of the Watom teeth with Pacific and Asiatic dentitions will be made later.

Non-metric dental features. A record of the original non-metric observations, including pathology, recorded in the Watom dentitions was made. Summaries of this information, along with the data recorded in other Lapita teeth, are presented in Tables 8 through 11.

The maxillary incisors typically exhibit slight shovelling. Mandibular incisors are almost never observed to be shovelled in these remains. Examples of peg-shaped teeth, enamel extension and Carabelli's cusp are not observed in the Watom teeth. A protostylid cusp, an accessory cusp found in mandibular molars, is observed in a single tooth. The "+4" configuration is the most common cusp pattern in the mandibular molars from Watom.

Dental pathology. The incidence of premortem and postmortem tooth loss in Watom and other Lapita teeth is presented in Table 9. A single mandible (Watom 3) accounts for the majority of premortem tooth loss observed in the Watom remains. Tooth loss in this mandible is restricted to the incisor and canine teeth.

The frequency of periodontal disease in Watom and other Lapita-associated dental remains is summarised in

Table 10. The majority of the Watom teeth exhibit calculus deposits and resorption of the alveolus bone suggestive of periodontal disease. Table 11 records the frequency of occurrence of other kinds of dental pathology recorded in the Watom and Lapita-associated teeth. Enamel hypoplasia is rarely observed in the dental remains from Watom. No examples of dental caries or abscessing are observed. Slight (affecting the enamel only) to moderate (dentin exposed) levels of attrition are observed in the Watom teeth. Some of the teeth of Watom Burial 6 are discoloured; the cause of this discolouration is indeterminate.

Infracranial Skeleton

The descriptive statistics for measurements recorded in the adult infracranial skeletons from Watom are set out in Tables 12. A summary of estimated stature and indices derived from the mean measurements are presented in Tables 13 and 14.

Stature estimates for six male skeletons range from 170 cm (5'7") to 180 cm (5'11"). Estimates of stature for the two females are 155 cm (5'1") and 164 cm (5'5"), respectively. According to the humeral diaphyseal index, the Watom male humeri are not flat. The forearm bones are long relative to the lengths of the upper arm bones. The shapes of the upper femur shafts in Watom males border on flattening (platymeria) but the mean value for this index indicates they are more rounded. The mid-shafts of the femora have medium to strong pilaster (well-marked linea aspera) development. The proximal tibial shafts approach eurycnemic (triangular) shapes.

A summary of the non-metric variation observed in the Watom and Tongan (Burial AK) infracranial skeletons is given in Table 15.

A costo-clavicular sulcus, located at the site where this ligament inserts on the inferior surface of the clavicle, is well developed in five of the six sides examined. Houghton (1980) attributes the latter feature to canoe paddling among Polynesians. A supraclavicular foramen is observed in two clavicles. A septal aperture, or perforation of the olecranon and coronoid fossae in the distal humerus, is observed in a single bone. Deep preauricular pitting (groove of pregnancy), is observed in the left innominate bone of Burial 1. An imprint of a ligament, in the same region, is observed in Watom Burial 3, a male. A Fossa of Allen, or cervical depression near the anterior superior margin of the femoral neck close to the head, is observed in a single femur. The fovea capitis, the site of attachment of the ligament for the head of the femur, is oval in shape in three of the five bones examined and round in shape in the remaining two specimens. A small depression (here called a facet) in the supero-lateral angle of the patella is present in ten of the twelve bones examined. No examples of Vastus notch, a larger indentation in the same region of the patella, are observed in the Watom remains. Spurring of the anterior surface of the patella is relatively common. Both tibial and talar squatting facets are observed in these remains. The anterior calcaneal facet is discrete in five of the nine bones examined. The peroneal tubercle,located on the anterior lateral surface of the calcaneus, is scored as present in two of the five bones examined.

A summary of non-metric variation recorded in the vertebral columns from Watom Island and Burial AK from Tonga are summarised in the Table 16. No unusual variation was observed in any of the vertebrae from Watom. No cases of spina bifida or spondylolysis were observed.

Photographic plates of some of the long limb bones from the Waton burials are shown in Plates 12–28.

Palaeopathology

Dental pathology is summarised in the section on teeth. In this section, a summary of osteoarthritis or degenerative changes in the articular surfaces of the infracranial skeleton are presented along with any other kinds of pathology observed in these remains.

Osteoarthritis. Observations on osteoarthritis in the limb and vertebral skeletons were made in the eight Watom burials. A summary of osteoarthritis in the appendicular skeleton is presented in Table 17. There is very little arthritic lipping in the Watom remains; the level of involvement generally does not exceed minimal levels of severity. Osteophytosis and degenerative changes in the vertebral column are of equally low occurrence.

Other pathology. Other examples of pathological bone in the Watom remains are relatively uncommon. Brief comments on the pathology observed in each of the eight burials are made in Table 1. Some of the pathology is summarised here.

Possible trauma and periostitis. The left fifth metacarpal of Burial 2, a young female aged between 18 and 20 years, exhibits slight callus formation about mid-shaft suggestive of a healed fracture (Plate 14). The fracture is well healed indicating the trauma had occurred at an early age. The proximal phalanx for the left second metacarpal from Watom Burial 3, a male aged 30 to 40 years, exhibits a possible healed fracture and periostitis at the proximal end (Plate 15). No x-rays were available to confirm these interpretations.

The proximal end of the left femur of Burial 6, a male whose age has been estimated to be about 30 to 35 years, is pathological (Plate 27). The entire subtrochanteric region is enlarged and the greater trochanter was probably loss postmortem. The rest of the femur is not involved. Differential diagnosis includes periostitis, or inflamation of the periosteum due to infection or traumatic injury, possibly a healed fracture, in the subtrochanteric region. Drainage cloacae are not present. The left femur is approximately 14 mm shorter than the left. Radiographs were not available.

Other. Enlarged nutrient foramina were observed in at least two metatarsal bones of two different burials (Plate 28).

Partial sacral hiatus was observed in the sacral fragment belonging to the remains of Burial 5. The right fibula of this same individual is unusually long and and exhibits localised swelling in the region where the peroneus brevis attaches. The soleal line in the left tibia of Burial 8 is especially well developed. The latter, while incomplete, appears to be longer than the right tibia. Some examples of dental pathology observed in the Watom remains are presented in Plates 2–6.

Comparisons

In this section I attempt to elucidate the biological relationships of the Watom Lapita remains through univariate and multivariate comparisons with other Oceanic skeletal samples including some of the extant Lapita skeletal samples. Some of the information recorded in other Lapita remains has been presented in the tables summarising the observations recorded in the Watom remains. New tables, containing information for other Pacific and Asiatic samples, are introduced in this section. Given the limited number of Lapita skeletons being compared, the conclusions reached must remain tentative.

Univariate comparisons. Comparing the mandibular measurements and indices (Table 4) recorded in the Watom and Lapita samples reveals some similarities. For example, the index of robustness, which measures the thickness of the mandibular body, is about the same in the Watom and Lakeba specimens. The shape of the ramus, as expressed by the ramus index, is similar for the Watom and Tongan (Burial AK) specimens. The mostly edentulous condition of the Natunuku mandible explains the relatively low mandibular height measurements recorded in this specimens. Comparing the Watom indices with other Pacific groups (Table 18) emphasises the distinctiveness of the Watom mandibles. The relatively broad mandibular shape, divergent and broad rami, immediately apparent when viewing the material for the first time, are not found in any of the Pacific and Asiatic (including Lapita) mandible series presented in Table 18.

A more uniform morphological picture emerges when the non-metric characteristics of the Watom and Lapita mandibles (Table 6) are assessed. Although observations are restricted, none of the mandibles possess a mylo-hyoid bridge. Multiple mental and mandibular foramina are never observed. These features, however, are relatively rare in most Pacific mandibles. Two of the Watom mandibles are classified as 'rocker jaws'. One additional Watom mandible and all remaining Lapita mandibles are classified as partial 'rockers' while a fourth Watom mandible is a non-rocker. Broader comparisons (Table 19) suggest the rate of occurrence of rocker jaw in the Lapita mandibles (including Watom) is intermediate between the Polynesian and Melanesian samples. In these comparisons, any expression of rocker jaw, full or partial, is recorded as present. One of the highest rates of occurrence for rocker jaw (and the majority are partial rockers) is recorded in the Papuan sample which consists largely of skulls from the Purari Delta, Gulf Province, Papua New Guinea.

Measurements and cross-sectional areas for Watom and Lapita teeth were presented in Table 7. Comparable, but incomplete, data are available for the Watom, Burial AK (Tonga), Natunuku and Manus specimens. The teeth of Burial AK are larger than those from Watom but this is not unexpected since modern Tongans have the largest teeth among Polynesians (Brace & Hinton, 1981). The Watom teeth, as measured by the tooth summary figure, are the smallest of any of the samples listed in Table 20. Other small toothed samples include the Chinese, Chatham Islanders, Borneo, Hawaii and Japan.

Non-metric dental variation recorded in the Lapita samples is given in Table 8. Peg-shaped teeth, enamel extensions and protostylid cusps are rare. Dental pathology is given in Tables 9 through 11. The occurrence of periodontal disease is about the same in the Watom and Tongan (Burial AK) Lapita samples. Caries are remarkably absent in the Watom teeth while twelve of the fourteen teeth in the Tongan specimen are carious.

Comparing infracranial indices for the Watom and Lapita samples (Table 14) suggests the shapes of the Watom tibial and femoral shafts are significantly different. The linea aspera in the Watom femora are not as well developed as those in the Natunuku and the Tongan femora nor is the upper femoral shaft in the Watom remains as flattened as it is in the Fijian and Tongan (Burial AK) specimens. Similarly, the shape of the tibial shaft at the level of the nutrient foramen in the Watom material is not as flat as it is in the Natunuku and Tongan (Burial AK) specimens. Assembling more comparative data (Table 21) indicates that the shapes of the lower limb bone shafts from Watom are most like those from prehistoric Tonga and Nebira. The latter is a site about 16 km inland from the coast near Port Moresby, Central Province, Papua New Guinea. The slenderness of the Watom limb bones is substantiated by the low value it receives for the femur robusticity index. Except for Fiji and Nebira, there are no additional data for Melanesian populations.

Examining stature, Polynesians are on average taller (170 cm) than Melanesians (160-165 cm). The estimates of stature for the Watom males (174 cm) are similar to Polynesians. However, the Tolai of the north-eastern Gazelle Peninsula of New Britain are as tall as the Watom people according to measurements made by von Luschan (1897) (and see Howells, 1970:210, 1973:164).

Although comparative data are generally lacking, the presence of costo-clavicular sulci, oval-shaped fovea capitis in the femoral heads and squatting facets in the Watom remains are consistent with the general morphological pattern seen in Pacific populations.

To summarise the univariate comparisons, the remains of Watom and Lapita people show similarities and differences when compared with other Pacific populations. The similarities with Pacific populations, especially Polynesians, include tall stature, presence of rocker jaw, shovel-shaped incisors, costo-clavicular sulci, oval-shaped fovea capitis and squatting facets. Evidence for periodontal disease and the lack of dental caries further coincide with a

dental pattern generally characteristic of Pacific populations. It should be emphasised, however, that none of these features are exclusive to Polynesians but are generally typical of most Pacific populations.

Differences include mandibles (especially from Watom) characterised as possessing broad divergent rami and short mandibular bodies. This latter combination is generally not seen in the mandibles of Pacific and Asiatic groups. The small tooth crown diameters and gracile lower limb bones observed in the Watom material are further without parallel among the inhabitants of the Pacific.

In conclusion, these comparisons, based on small samples, provide little in the way of definite conclusions regarding the biological relationships of Watom and Lapita human remains and other Pacific groups.

Multivariate comparisons. Because the conclusions reached regarding biological relatedness based on univariate statistics are indefinite, multivariate methods are next considered. Multivariate statistical procedures provide researchers with some of the most objective means now available for describing and quantifying biological relationships and patterns of intergroup variation. For a discussion of the meaning and some of the limitations of these methods, the reader is directed to Howells (1969, 1972, 1973), Corruccini (1975), Kowalski (1972), van Vark (1976) and van Vark & Howells (1984).

Two multivariate procedures, stepwise discriminant function analysis and Mahalanobis Generalized Distance (Mahalanobis, 1936) are applied to measurements recorded in Lapita mandibles, including those from Watom, and more modern Pacific samples. The mandible is the most numerous and complete bone present in these remains and hence its selection for multivariate comparisons. The computer program BMDP-7M was used to do the stepwise discriminant function analysis (Dixon & Brown, 1979). Tree diagrams were constructed applying the unweighted pair-group clustering technique.

Two separate analyses are made; one uses seven samples and 22 mandibular measurements and the another uses eight samples and four mandibular measurements. The means and standard deviations of the 22 mandibular measurements are given in Table 22. With the exception of the Lapita sample, these data are the same as those used in Pietrusewsky (1985b). The Lapita sample in the present study includes measurements recorded in three Watom mandibles and individual specimens from Tonga, Manus, Lakeba and Natunuku.

Missing measurements for the Lapita mandibles were replaced by mean scores calculated for the entire sample. Missing measurements for individual specimens in each of the remaining six samples were replaced by regressed values generated for each group by the stepwise regression program, PAM (Dixon & Brown, 1979). The means and standard deviations for the four measurements used in the second analysis are presented in Table 28.

Analysis I (seven samples, 22 measurements). *Stepwise discriminant analysis.* A ranking of the 22 measurements for seven male samples, according to the F-values received in the final step of discriminant function analysis, is set out in Table 23. Mandibular length, mid-condylar width, symphysis height, bicondylar breadth and the width of the mandibular body at the mental foramen rank high in this analysis.

Eigenvalues and the percentage of dispersion for each of the six canonical variables are presented in the next table (Table 24). The first three functions account for nearly 80 percent of the total variance.

Canonical coefficients, arranged in decreasing order, for the first two functions are presented in Table 25. Bicondylar width, length of the mandible, ramus breadth and symphyseal height of the mandibular body are important discriminators in the first function.

The assignment values achieved at the end of the stepping process are arranged in Table 26. The percentage of correct classifications is very high. One Maori and one Tongan specimen each are misclassified as Northern Marianas. One of the Wairau Bar mandibles is misclassified as a New Zealand Maori. Fig. 1 is a plot of seven group centroids on the first two functions. The Lapita centroid falls outside the loose constellation which forms between the Polynesian and Micronesian samples. New Zealand and Chatham Islands are set off from the remaining groups.

Generalised distance. Mahalanobis' Generalised Distance is applied to six measurements which are found to produce the greatest discrimination in the previous analysis. The distances are set out in Table 27. A cluster analysis of the distances is shown in Fig. 2. The Lapita sample is the last to join the grouping after all the Polynesian and Micronesian samples have clustered. New Zealand (Maori) and Chatham Islands (Moriori) form a tight cluster to which Namu is attracted. Tonga, Northern Marianas and Wairau Bar form a second major cluster.

In summary, this analysis, based on the largest number of mandibular measurements available for analysis, fails to place Lapita with prehistoric or more modern Polynesian or Micronesian (Chamorro) samples. The analysis does distinguish, however, a recognisable Lapita grouping. Mandibular length, bicondylar width and symphyseal height account for most of the differences produced.

Analysis II (eight samples, four measurements). In this analysis the same multivariate procedures are applied to a more diverse sampling of mandibles representing populations from the Pacific and the Asiatic mainland. The set of measurements is reduced to four, the largest subset available for the groups sampled. Table 35 gives the means and standard deviations for the four measurements for each group. Smaller samples have been consolidated to form the groups presented. Group membership is explained at the bottom of Table 28. Some of these data have been used in previous investigations of the Lapita remains from Natunuku while others are being presented for the first time.

Stepwise discriminant function analysis. A ranking of the four measurements according to the F-values received in the final step of discriminant function analysis is presented in Table 29. The breadth of the ramus is the most important

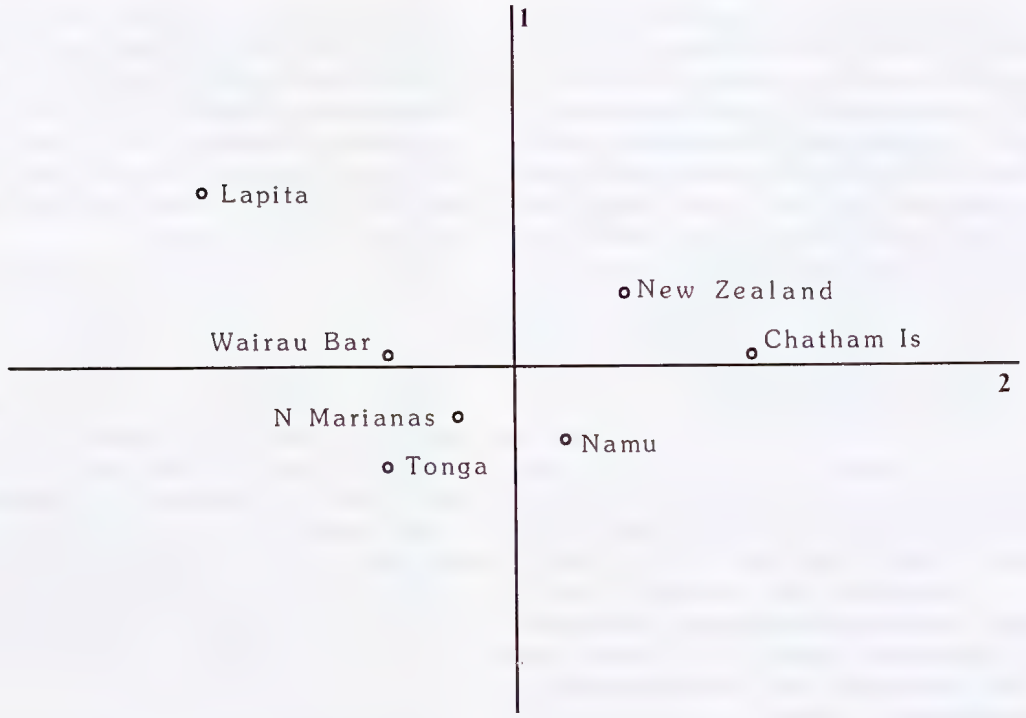

Fig.1. Plot of 7 male centroids on the first two discriminant functions.

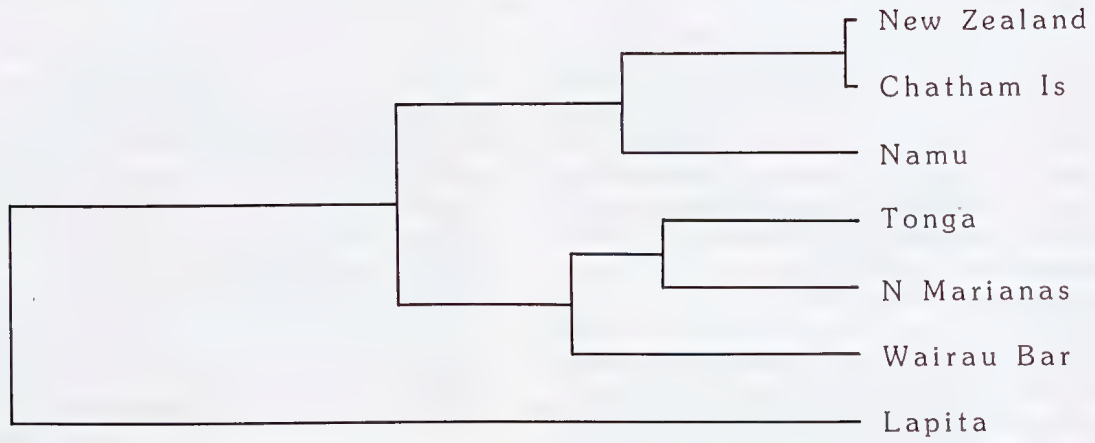

Fig.2. Diagram of relationship based on a cluster analysis of d-squared results based on 6 mandibular measurements.

variable and accounts for much of the discrimination produced. Eigenvalues and the precentage of dispersion are given in Table 30. The first two functions are responsible for nearly 90 percent of the total variance. Canonical coefficients for the first two functions (Table 31), arranged in decreasing magnitude, further indicate ramus breadth and symphysis height are the two most important discriminators. A summary of the classification results achieved at the end of the stepping process are given in Table 32. Generally, these classification results are poor. The highest number of correct classifications are those obtained by the Lapita sample.

Fig. 3 is a plot of group centroids on the first two functions. The Lapita and eastern Melanesian centroids form a cluster while Polynesian, South-east Asian and East Asian centroids form a separate cluster. The Papuan and Bismarck Archipelago centroids occupy peripheral positions in the diagram. Plots of individual Lapita cases (not shown) indicate the greatest overlap is between the three Watom specimens and eastern Melanesia and secondarily with Polynesian cases. The Manus and Tongan (Burial AK) specimens follow a similar pattern of association. This program further calculates Mahalanobis' d-squared and the posterior probability values for each case after the final step of the discriminant analysis, and indicates on the basis of these scores any incorrect classifications. One of the Watom mandibles (Watom 3), for example, is misclassified as a Polynesian and Watom 6 is incorrectly classified as an

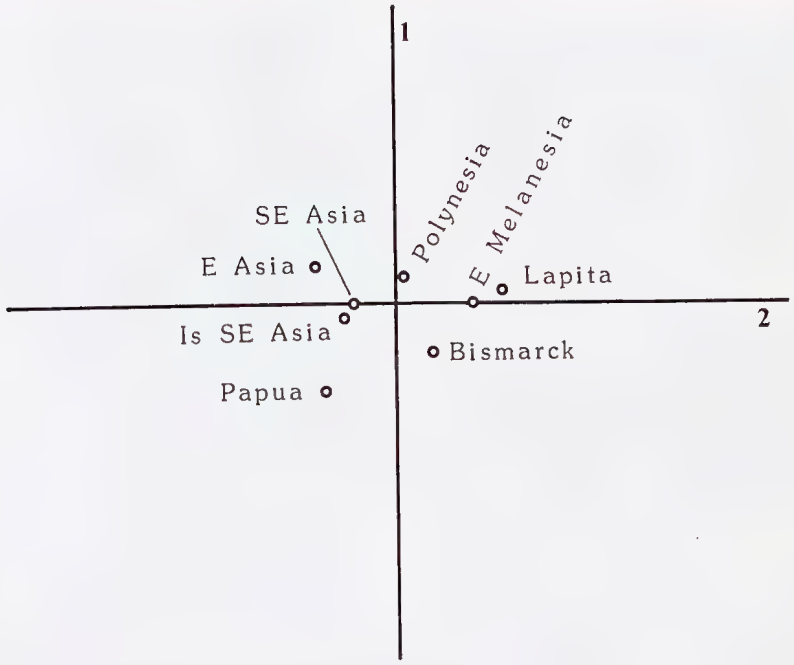

Fig.3. Plot of 8 group centroids on the first two discriminant functions.

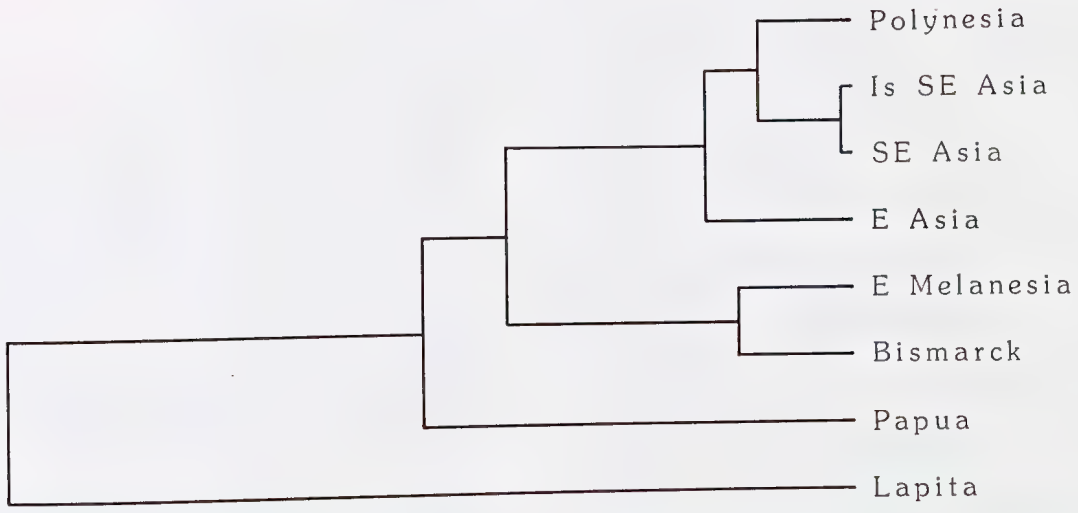

Fig.4. Diagram of relationship based on a cluster analysis of d-squared results based on 4 mandibular measurements.

eastern Melanesian.

Generalised distance. The results of applying Mahalanobis' Generalised Distance to four mandibular measurements recorded in eight male samples are presented in Table 33. The greatest distances are those between Lapita and all other groups. Fig. 4 is the diagram of relationship which results from a cluster analysis of the d-squared results. Polynesian, two South-east Asian and an East Asian sample form a cluster separate from one which includes the eastern Melanesian and Bismarck Archipelago samples. Papua and Lapita, in that order, connect after the latter two groups cluster. Inspection of the original d-squared values in Table 33 suggests that while Lapita is generally far removed from all groups, it is relatively closest to the eastern Melanesian sample followed by the Polynesian and Bismarck samples. In the cluster analysis, however, these associations are no longer evident due to the very close connection which forms between the remaining groups.

This second multivariate analysis reiterates the distinctiveness of the Lapita mandibles and groups Polynesians with South-east Asian and East Asian samples. Plots of the group centroids on the first and second functions suggests a weak association between Lapita, eastern Melanesian and Polynesian means. Ramus breadth and the height of the symphysis are responsible for most of

the discrimination produced.

While limited to a few measurements recorded in mandibles, the results of the present multivariate analysis reinforce the isolation of the Lapita mandibles suggested in the univariate analyses. The multivariate analyses further hint at an eastern Melanesian (and possibly Polynesian) connection. Ramus breadth and symphyseal height emerge as the most important discriminators.

Summary and Conclusions

Eight adult (six male and two female) individuals are represented in the skeletal remains from Watom Island. With the exception of a single young (18 to 20 years of age) female, all individuals died between approximately 30 and 35 years of age. None of the major burials are subadults. The remains are in a generally poor state of preservation with only a few intact long limb bones represented. Four mandibles, of varying states of completeness, are further identified in these remains. Six of the eight major burials have no cranial remains. An inventory of miscellaneous human remains found at the site, some of which could be assigned to the major burials, is further made.

Measurements and non-metric observations recorded in all skeletal and dental remains from the Watom site are summarised by anatomical region. The mandibles are typically broad and short. Broad divergent ascending rami are further characteristic of the mandibles. With one exception, all the mandibles are classified as rocker jaws. The Watom teeth are unusually small and the incisors are slightly shovelled. While the teeth are generally caries free, there is evidence for periodontal disease and slight to moderate dental wear.

Stature estimates for the Watom male specimens fall into the tall category (174 cm). The long limb bones are typically long and gracile. Costo-clavicular sulci, oval-shaped fovea capitis and squatting facets are further common in the remains from Watom.

There is little or no osteoarthritis or osteophytosis in the Watom remains. Possible healed fractures are observed in hand and finger bones of two individuals. The proximal end of one femur exhibits periostitis, possibly the result of a traumatic (healed fracture) injury.

Limited univariate comparisons indicate morphological similarities (e.g. rocker jaw, tall stature, costo-clavicular sulci etc.) between the Watom and Lapita people and other inhabitants of the Pacific and Polynesia but further reveal a number of biological differences such as small teeth, slender lower long limb bones and short broad mandibles which are generally not found in Pacific Islanders. Multivariate analyses, using mandibular measurements, generally separate the Watom and Lapita mandibles from other Pacific and Asiatic groups but hint of a possible biological connection with eastern Melanesian (and possibly Polynesian) populations. These conclusions should be viewed as tentative until much larger, and earlier dated, Lapita-associated skeletal samples become available.

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Appendix A

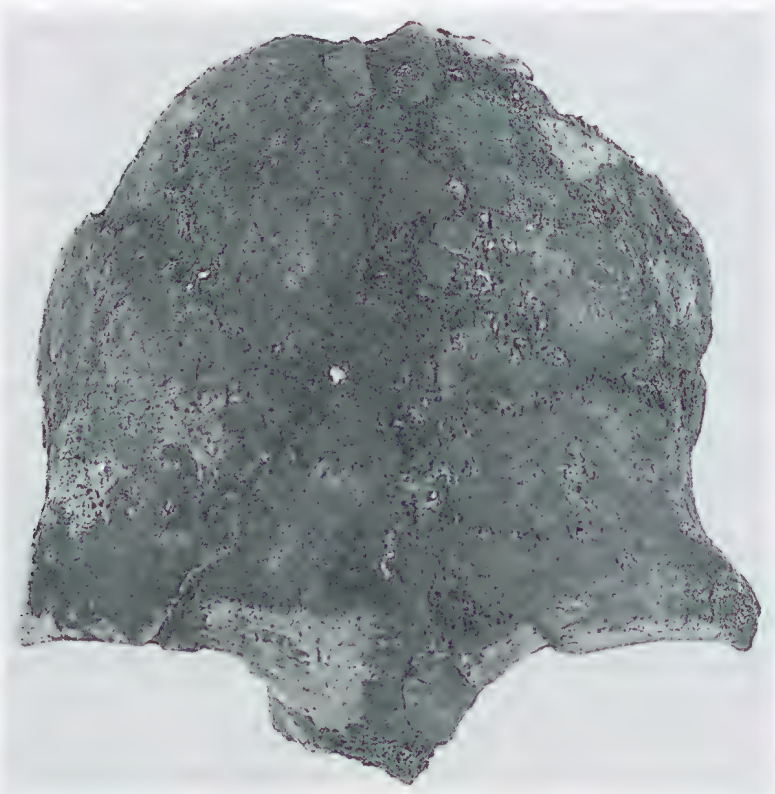

Plate 1. Frontal bone of Burial 3. The skull of this burial, while fragmented, is one of the most complete crania from Watom.

Plate 2. Occlusal view of the mandible of Burial 3 from Watom. The teeth exhibit moderate wear. Some of the anterior teeth were lost before death. There are no caries or dental abscessing. The "+4" pattern is the predominant molar cusp pattern in this specimen.

Plate 3. Frontal view of the mandible of Burial 3. There is postmortem damage in the symphysis region.

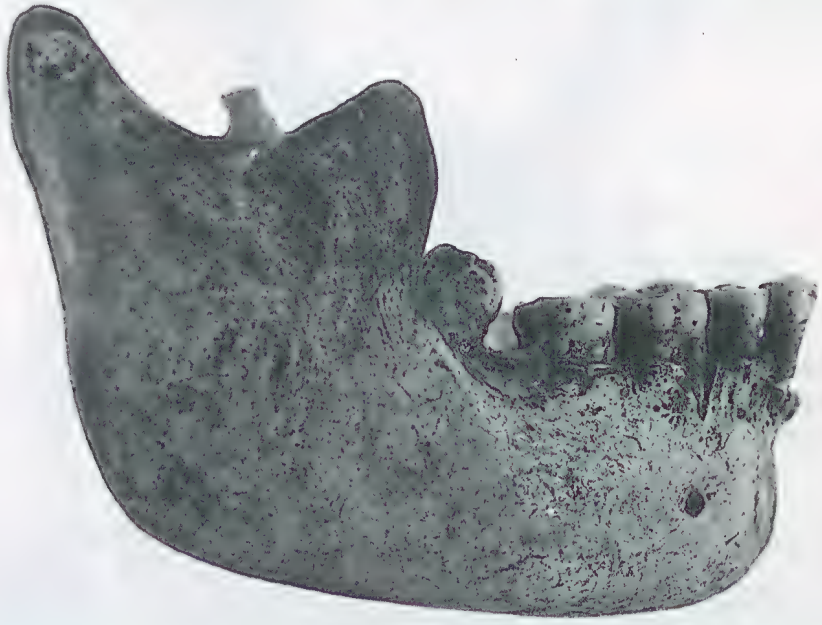

Plate 4. Lateral (right) view of the mandible of Burial 3. The ramus is low and broad and the body is short. The rocker jaw condition is present. The mental foramen is single.

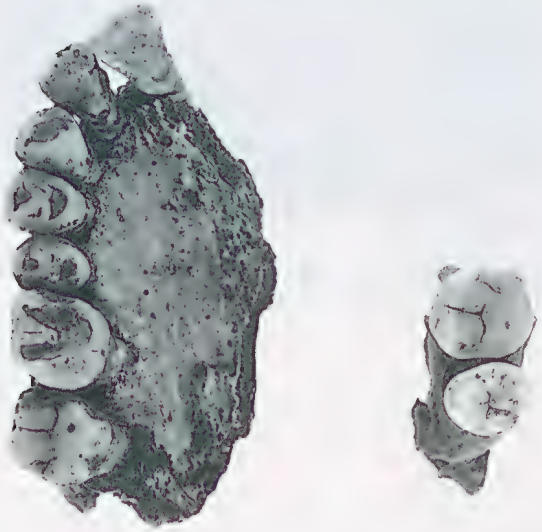

Plate 5. Occlusal view of the two maxillary fragments of Burial 3 from Watom. Tooth wear has exposed the dentin.

Plate 6. Lateral view of the right maxilla fragment of Burial 3. The enamel and roots of the teeth are stained.

Plate 7. Occlusal view of the mandible belonging to Watom Burial 6. The superior portion of the right ramus is damaged and missing. There is tooth crowding in the incisor region. The dentin is exposed in some of the teeth.

Plate 8. Frontal view of the damaged mandible of Watom Burial 6. Encrustations are visible in the anterior teeth.

Plate 9. Lateral (left) view of Watom Burial 6 mandible. The mandible is not a rocker jaw. Note the broad ramus.

Plate 10. Occlusal view of two maxilla fragments of Watom Burial 6. The left third molar is reduced in size.

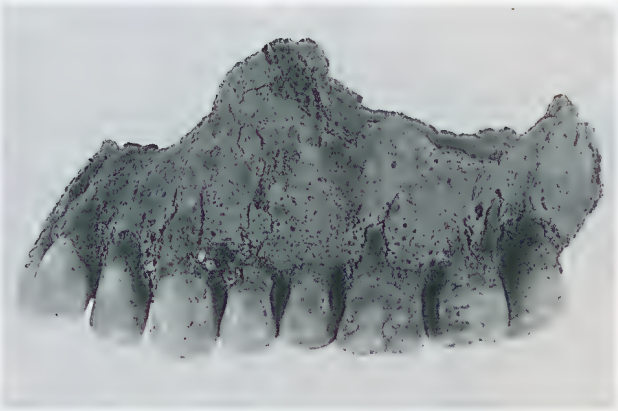

Plate 11. Lateral view of the left maxilla fragment of Watom Burial #6. There is some discolouration of the enamel.

Plate 12. Some of the long limb bones belonging to Watom Burial 2.

Plate 13. Shaft fragments of the left radius and ulna of Watom Burial 2. The interosseous border of the radius, where the abductor pollicis longus attaches, is strongly developed. The same area in the right radius is less strongly developed.

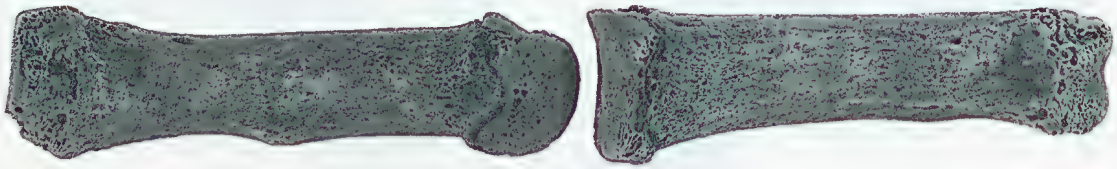

Plate 14. The left fifth metacarpal and proximal phalanx of Watom Burial 2. The metacarpal exhibits a possible healed fracture about mid-shaft. The epiphyseal line of fusion is still evident.

Plate 15. Anterior (A) and posterior (B) views of the left second metacarpal and proximal phalanx of Watom Burial 3. The proximal end of the phalanx is misaligned and exhibits a possible healed fracture and periostitis. Swelling and porosity are further evident.

Plate 16. Some of the major infracranial bones and bone fragments from Watom Burial 4.

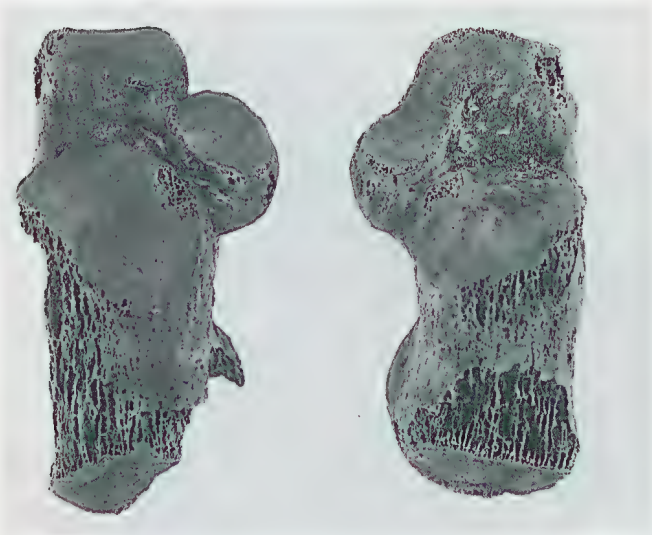

Plate 17. Right and left calcanei of Watom Burial 4. The anterior and middle articular surfaces for the talus are separate on the left. The same surfaces are connected and hour-glass-shaped on the right.

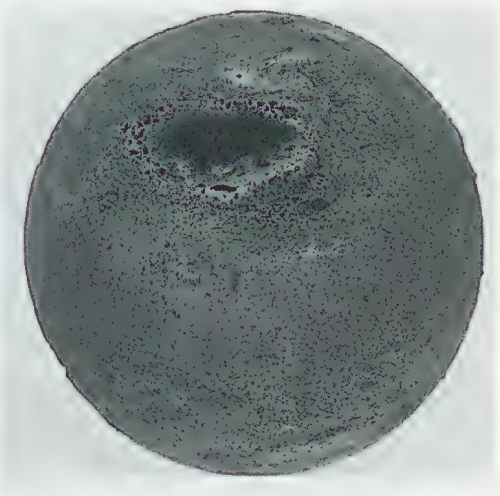

Plate 18. The head of the right femur of Watom Burial 4 showing an oval-shaped fovea capitis, the site of attachment for the ligament for the femur head.

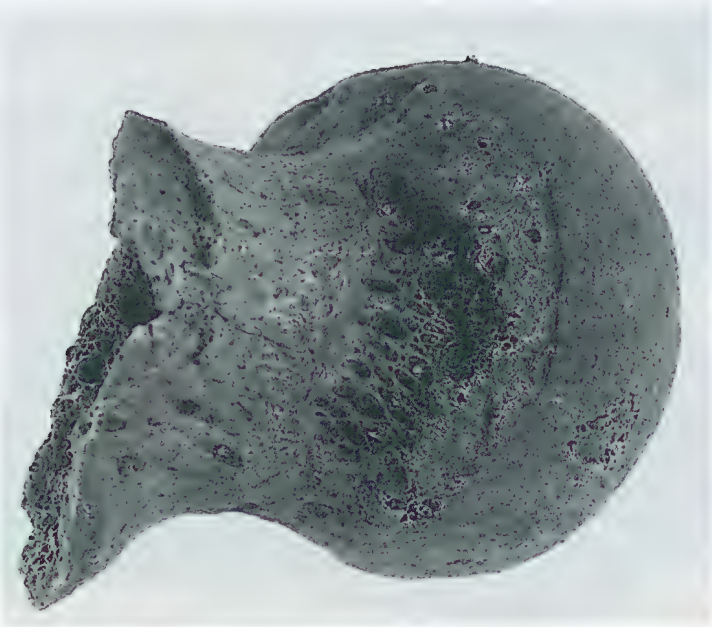

Plate 19. The head and neck region of the right femur of Watom Burial 5 exhibiting a Fossa of Allen or cervical fossa in the anterior superior margin of the femoral neck. The underlying trabeculae are exposed.

Plate 20. Fragment of the posterior region of the sacrum of Watom Burial 5 exhibiting sacral hiatus.

Plate 21. Left talus of Watom Burial 5 exhibiting a squatting facet in the neck region.

Plate 22. Some of the major upper limb bones and fragments of Watom Burial 6. With the exception of the skull, this is the most complete and best preserved skeleton from Watom.

Plate 23. Overview of some of the major lower limb bones from Watom Burial 6.

Plate 24. Hand bones from Watom Burial 6.

Plate 25. Foot bones from Watom Burial 6.

Plate 26. (A) Inferior surface of the right clavicle of Watom Burial 6. The impression for the costoclavicular ligament is deepened into a sulcus. A facet is visible in the region of the trapezoid line at the lateral end of the same bone. (B) Superior surface of the right clavicle of Watom Burial 6.

Plate 27. (A) Anterior view of the proximal end of the left femur of Watom Burial 6 exhibiting a possible healed fracture with extensive periostitis. (B) Posterior view of the proximal end of the left femur from Watom Burial 6. There is postmortem damage in the region of the greater trochanter.

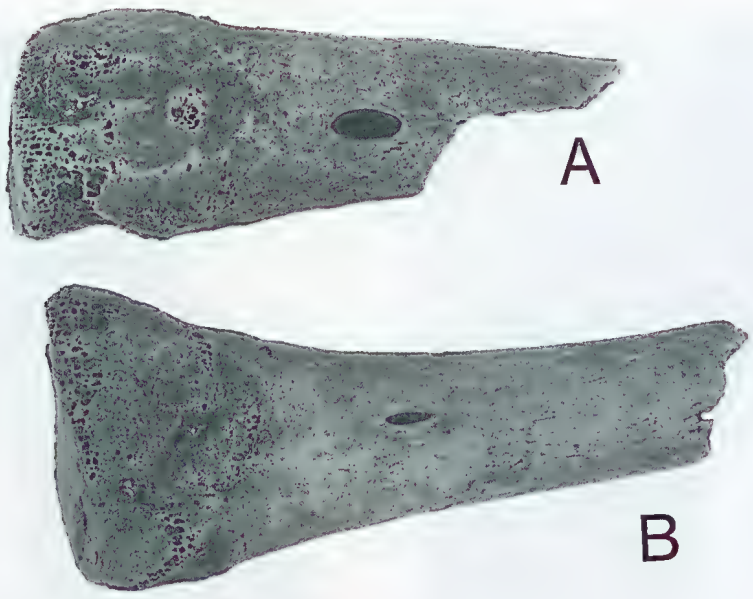

Plate 28. (A) Lateral view of the right third metatarsal found intrusively with Watom Burial 7. (B) Lateral view of the left fourth metatarsal of Watom Burial 6. Both metatarsals exhibit enlarged nutrient foramina.

Plate 29. Right lateral view of the mandible and portion of the right temporal bone of Burial AK, a Lapita-associated skeleton from Tongatapu, Tonga. The right condyle is pathological but articulates with the right temporal fragment. The lower first premolar is carious. The alveolar margins exhibit considerable resorption.

Plate 30. Occlusal view of the maxilla and mandible fragments of Burial AK. Many of the teeth, not loss premortem are worn and carious.

Appendix B

Table 1. Individual Descriptions of Watom Burials.

Site SAC (Site 8)

Burial No.: 1
Provenience (Excavator, year, rectangle): Specht, 1966, Rect. I
Age: 30 years (auricular surface, degeneration).
Sex: Female (sciatic notch, pre-auricular sulcus and femoral head diam.).
Stature: 164 cm (5'5") The length of the right femur was estimated to be 42.9 cm using Steele's (1970) segment measurement No. 1 (7.7 cm); stature was estimated using formula No. 1 of Houghton *et al.* (1975).
Completeness: No skull. Infracranial skeleton is substantially incomplete and many bones are broken. Except for patellae and some hand and foot bones, none of the limb bones are complete.
Intrusive human remains: Right fourth metacarpal.
Preservation: Fair. The hand and foot bones and patellae are the best preserved bones. Bones are light in weight. Some reconstruction was achieved.
Pathology: There is little or no osteoarthritis in these remains.
Anomalies: An anomalous foramen was observed on the inferior surface of the right clavicle anterior to the site of attachment for the conoid ligament. The site of attachment of the deltoid muscles on the superior surfaces of both clavicles is well developed.
Comments: Tibiae, right fibula and patella and some hand and foot bones were assigned to this individual from associated miscellaneous material. Some lower long limb bone fragments were sacrificed for chemical analyses prior to this study.

Burial No.: 2
Provenience (Excavator, year, rectangle): Specht, 1966, Rect. I/III
Age: 18-20 years (the distal epiphysis of the fifth metacarpal exhibits recent fusion)
Sex: Female (sciatic notch, size and muscle markings).
Stature: 154.7 cm. (5'1") Segment No. 2 (21.1 cm) of the left femur yielded a maximum length of 38.7 cm. (Steele 1970). Stature was estimated using Houghton *et al.* (1975) formula No. 7.
Completeness: No skull. Infracranial skeleton is represented by forearm and bones of the lower limb skeleton, a fragment of the right innominate and a single lumbar vertebra fragment. Hands and feet are relatively incomplete.
Preservation: Fair/Good.
Pathology: Possible healed fracture of left fifth metacarpal bone. There is no osteoarthritis in the appendicular skeleton.
Anomalies: Interosseous borders of both radii are extremely well developed. The soleal line on the posterior surface of the right tibia exhibits a raised roughened prominence at its commencement.
Comments: A box, previously unopened before this study, contained the distal ends of the right fibula and ulna and several metapodial bones.

Burial No.: 3
Provenience (Excavator, year, rectangle): Specht, 1966, Rect. I
Age: 30-40 years (dental attrition and degeneration).
Sex: Male (some pelvic indicators, sciatic notch and pre-auricular sulcus, suggest the sex is female while the lower limb bones indicate male. The skull possesses predominantly male features).
Stature: 176.2 cm (5'9") Stature was estimated using the right femur segment measurement No. 4 (3.9 cm) and Houghton *et al.* (1975) formula No. 1.
Completeness: Partial skull and very fragmentary infracranial skeleton. The most intact portions of the latter include the hand and foot skeletons, and shafts of the right humerus and both femora. The skull is in pieces, some of which have solidified into a calcified mass. The right parietal is warped. The most complete bones of the skull include the frontal, right parietal and right zygoma. Large portions of the left parietal and temporal bones, a mandible, occipital fragment and right maxilla containing teeth are further preserved.
Preservation: Fair/Poor. Concretions have solidified major portions of the cranial vault.
Pathology: Periodontal disease but no dental caries; there is little or no osteoarthritis.
Anomalies: Alveolar prognathism.
Comments: Fibula and some limb bone shaft fragments were removed for chemical analyses prior to this study. Several hand and foot bones were assigned to this burial from miscellaneous material. The mandible is robust and is classified as a rocker jaw.

Burial No.: 4
Provenience (Excavator, year, rectangle): Green & Anson, 1985, Rect I/IV
Age: 35 (based on McKern & Stewart (1957) symphysis pubis aging method: 23-39 years and lack of extensive degeneration).
Sex: Male (pelvic indicators: narrow sciatic notch and absence of pre-auricular sulcus and parturition pits; femoral head diameter).
Stature: 170 cm (5'7") Stature was estimated using the right femur segment measurement No. 2 (23.5 cm) and Houghton *et al.* (1975) formula No. 1.

Completeness: No skull. Infracranial skeleton is substantially complete but fragmentary. Forearm bones, left tibia, sternum and right patella are missing. Only some of the hand and foot bones are completely intact.
Preservation: Fair/Poor. The right humerus and both femora, and the hand and foot bones are best preserved.
Pathology: Some osteoarthritis is present in the infracranial skeleton.
Anomalies:
Comments: Material required extensive cleaning and mending before being studied. A small bag of bones labeled, "bones from burial at west and centre part. May 22, 1985 Burial 4(?)", which include the right metacarpals 1, 2 and 4 and a portion of the atlas vertebra, belong to this burial. Fibula fragments were removed for chemical analyses prior to this study.

Burial No.: 5
Provenience (Excavator, year, rectangle): Green & Anson, 1985, Rect I/III
Age: 30 years (auricular surface, sternal end of rib).
Sex: Male (sciatic notch, absence of pre-auricular sulcus; limb bone diameters).
Stature: 173.7 cm (5'8") Stature was based on the maximum length of the left humerus (32.5 cm) and Houghton *et al.* (1975) formula No. 10.
Completeness: No skull. Infracranial skeleton represented by fragments of humeri, right femur, fibulae, patellae, left clavicle, scapulae, vertebrae, innominates, hands and feet.
Intrusive human remains: Left talus, left second cuneiform, left navicular fragment, left patella, fragment of left acetabulum, right proximal phalanx of first metatarsal, and metacarpals 2 through 5 from right hand.
Preservation: Good/Fair. Once encrustations were removed, the hands, feet, left humerus, right fibula and major portions of the innominate bones were found to be well preserved.
Pathology: Partial sacral hiatus; there is little or no osteoarthritis.
Anomalies: Right fibula is unusually long and exhibits swelling in the region of the peroneus brevis attachment at the proximal end of this bone. A Fossa of Allen is present in the right femur.
Comments: Rib fragments and several fibula fragments were removed for chemical analyses prior to this study. Animal bones and teeth, obsidian and pot sherds were found associated with these remains at the time of this study.

Burial No.: 6
Provenience (Excavator, year, rectangle): Green & Anson, 1985, Rect. III
Age: 30-35 years (lack of osteoarthritis, slight to moderate dental wear).
Sex: Male (sciatic notch , mastoid and general bone size indicate male).
Stature: 180 cm (5'11") based on maximum length of left humerus (35.0 cm) and Houghton *et al.* (1975) formula No. 10.
Completeness: Partial cranium and substantially complete mandible. The infracranial skeleton is substantially complete, only the right fibula, some hand and foot bones, sacrum, and most of the sternum are missing. The left arm limb bones, clavicles and right radius are complete.
Preservation: Good. This is the best preserved burial. Bones were mended (re-mended) after a thorough washing.
Pathology: Proximal end of left femur exhibits extensive reactive bone formation and periosteal inflamation. No dental caries but there is evidence of peridontal disease and slight to moderate degrees of dental attrition in the teeth.
Anomalies: The teeth exhibit some discolouration, and there is tooth crowding. The mandible is not a rocker jaw. The fourth metatarsal possesses an enlarged nutrient foramen.
Comments: Most of the ribs have been sacrificed for citrate analysis.

Burial No.: 7
Provenience (Excavator, year, rectangle): Green & Anson, 1985, Rect III/IV
Age: Adult
Sex: Male (the limb bones are large)
Stature: 172.7 cm (5'8") Stature is based on right femur segment No. 2 (24.8 cm) and Houghton *et al.* (1975) formula No. 1.
Completeness: The cranium is represented by sixteen small fragments. The infracranial skeleton is represented by fragments of right scapula, vertebrae, right and left radius, distal end of right ulna, right femur, patella, right and left fibulae, right (?) tibia and some hand and foot bones.
Intrusive human remains: Left calcaneus, right third metatarsal fragment and an isolated premolar.
Preservation: Fair. Some reconstruction was attempted after washing.
Pathology: Slight osteoarthritis is present in the hand and foot bones.
Anomalies: An enlarged nutrient foramen was observed in an intrusive metatarsal (MT3) found with this burial.
Comments: Animal remains were found to be associated with this burial. Two human tarsal bones (left navicular and a third cuneiform) were assigned to this burial from the miscellaneous material. Fibula fragments were removed for chemical analyses prior to this study.

Burial No.: 8
Provenience (Excavator, year, rectangle): Green & Anson, 1985, Rect I/IV

Age: Adult (approx. 35 years).
Sex: Male (the limb bones are large).
Stature: 171.9 cm (5'7") based on left tibia segment No. 3 (13.6 cm) and Houghton *et al.* (1975) formula No. 8.
Completeness: No skull. Scapula and vertebra fragments represent the upper axial skeleton. The rest of the upper limb skeleton is missing. The lower limb skeleton is substantially complete but fragmentary.
Preservation: Fair. Remains were washed and reconstructed. The right foot is the best preserved part of the skeleton.
Pathology: Slight osteoarthritis in the limb skeleton.
Anomalies: The soleal line on the left tibia is very prominent. The left tibia appears to be larger than the right tibia.
Comments: Tibiae were treated with a 7% acetic acid solution to remove encrustations. The right scapula fragment, right femur, patella fragments and some hand and foot bones were assigned to this burial from associated miscellaneous material.

Table 2. Measurements recorded in crania from Watom Island and their descriptive statistics.

	Burial No.			Watom	
Variable[1]	3	6	N	Mean	S.D.
MAXFRONB	101		1	101.0	
MINFRONB	94		1	94.0	
BISTEPHB	87		1	87.0	
NASALBTH	26		1	26.0	
ALVEOLAL	59	61	2	60.0	1.4
MASTOIDH		31	1	31.0	
MASTOIDW		19	1	19.0	
BIORBITB	103		1	103.0	
INTERORB	31		1	31.0	
MALRLINF	26	44	2	35.0	12.7
MALRLMAX	39	55	2	47.0	11.3
CHEEKHGT	25	23	2	24.0	1.4
NASIBGCR	106		1	106.0	1.4
BRGLMDCR	92		1	92.0	
NASFROSB	14		1	14.0	

[1] MAXFRONB = Maximum frontal breadth, MINFRONB = Minimum frontal breadth, BISTEPHB = Bistephanic breadth, NASALBTH = Nasal breadth, ALVEOLAL = Alveolar length, MASTOIDH = Mastoid height, MASTOIDW = Mastoid width, BIORBITB = Biorbital breadth, INTERORB = Interorbital breadth, MALRLINF = Inferior malar length, MALRLMAX = Maximum malar length, CHEEKHGT = Cheek height, NASIBGCR = Nasion-bregma chord, BRGLMDCR = Bregma-lambda chord, NASFROSB = Nasio-frontal subtense.

Table 3. Measurements recorded in Lapita mandibles.

	Watom				Lakeba		Manus	Natunuku	Tonga
	3	6	M1	M2	1	2			
Mandibular length	96	91						108	
Inferior length	53	74		65	64		65	68	60
Alveolar length	58	49		66			64	71	54
Bicondylar width	139							114	
Bicondylar articular breadth	123								
Bicoronoid breadth	100	88							
Bigonial breadth	108	97						100	100
Bicanine external breadth	34	31					35	37	31
Bimolar-1 external breadth	62	56					68		61
Bimolar-3 external breadth	74	65					80		73
Symphyseal height	36	29	26	30	28	30	28	26	27
Mental foramen height	33	29	31	28	28	32	29	19	29
Canine height at C/P3	34	28	30	29	29	32	30	22	28
Molar height at M1/M2	30	27	30	27	28	29	27		26
Symphyseal breadth	15	12	15	12	14	13	16	14	14
Mental foramen breadth	13	10	12	11	11	11	12	11	10
Canine breadth	12	11	14	11	10	9	13	12	11
Molar breadth	16	13	15	13	13	13	14	13	14
Ramus height	65	72		51				60	61
Ramus breadth	43	44		41	31			33	41
Mandibular notch breadth	45	37						37	
Condyle length	11	10	11						
Condyle breadth	17	22	19						
P3-M1 length	25	22	22	26	15	14	30		26
M1-M2 length	23	20		23	18		23		
M1-M3 length	37	33		33			38		

Table 4. Descriptive statistics for measurements and indices recorded in male Lapita-associated mandibles.

	Watom			Lakeba			Natunuku	
Variable[1]	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.
MANDLNTH	2	93.5	3.5	0			1	108.0	
INFMANDL	3	64.0	10.5	1	64.0		1	68.0	
ALVEOLGT	3	57.7	8.5	0			1	71.0	
BICONDWH	1	139.0		0			1	114.0	
MIDCONDW	1	123.0		0			0		
CORONBTH	2	94.0	8.5	0			0		
BIGONIAL	2	102.5	7.8	0			1	100.0	
BICANBTH	2	32.5	2.1	0			1	37.0	
FRMOLBTH	2	59.0	4.2	0			0		
THMOLBTH	2	69.5	6.4	0			0		
SYMPHYHT	4	30.3	4.2	2	29.0	1.4	1	26.0	
MENFORHT	4	30.3	2.2	2	30.0	2.8	1	19.0	
CANINEHT	4	30.3	2.6	2	30.5	2.1	1	22.0	
MOLARHT	4	28.5	1.7	2	28.5	0.7	0		
SYMPHYBH	4	13.5	1.7	2	13.5	0.7	1	14.0	
MENFORBH	4	11.5	1.3	2	11.0	0.0	1	11.0	
CANINEBH	4	12.0	1.4	2	9.5	0.7	1	12.0	
MOLARBH	4	14.3	1.5	2	13.0	0.0	1	13.0	
RAMUSHGT	3	62.7	10.7	0			1	60.0	
RAMUSBTH	3	42.7	1.5	1	31.0		1	33.0	
MANDNOTB	2	41.0	5.7	0			1	37.0	
CONDYLGT	3	10.7	0.6	0			0		
CONDBTH	3	19.3	2.5	0			0		
PMMOLARL	4	23.8	2.1	2	14.5	0.7	0		
MONETWO	3	22.0	1.7	1	18.0		0		
MONETHRE	3	34.3	2.3	0			0		
MANDINDX	1	69.1		0			1	94.7	
GONCONDX	1	77.7		0			1	87.7	
RAMUSIND	3	69.2	10.0	0			1	55.0	
ROBUST	4	38.0	2.3	2	36.8	3.5	1	57.9	

	Tonga(AK)			Manus			Combined (All Lapita Mandibles)		
Variable	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.
MANDLNTH	0			0			3	98.3	8.7
INFMANDL	1	60.0		1	65.0		7	64.1	6.5
ALVEOLGT	1	54.0		1	64.0		6	60.3	8.2
BICONDWH	0			0			2	126.5	17.7
MIDCONDW	0			0			1	123.0	
CORONBTH	0			0			2	94.0	8.5
BIGONIAL	1	100.0		0			4	101.3	4.7
BICANBTH	1	31.0		1	35.0		5	33.6	2.6
FRMOLBTH	1	61.0		1	68.0		4	61.8	4.9
THMOLBTH	1	73.0		1	80.0		4	73.0	6.2
SYMPHYHT	1	27.0		1	28.0		9	28.9	3.1
MENFORHT	1	29.0		1	29.0		9	28.7	4.0
CANINEHT	1	28.0		1	30.0		9	29.1	3.3
MOLARHT	1	26.0		1	27.0		8	28.0	1.5
SYMPHYBH	1	14.0		1	16.0		9	13.9	1.4
MENFORBH	1	10.0		1	12.0		9	11.2	1.0
CANINEBH	1	11.0		1	13.0		9	11.4	1.5
MOLARBH	1	14.0		1	14.0		9	13.8	1.1
RAMUSHGT	1	61.0		0			5	61.8	7.7
RAMUSBTH	1	41.0		0			6	38.8	5.5
MANDNOTB	0			0			3	39.7	4.6
CONDYLGT	0			0			3	10.7	0.6
CONDBTH	0			0			3	19.3	2.5
PMMOLARL	1	26.0		1	30.0		8	22.5	5.6
MONETWO	0			1	23.0		5	21.4	2.3
MONETHRE	0			1	38.0		4	35.3	2.6

Table 4 (cont'd).

Variable	Tonga(AK) N	Mean	S.D.	Manus N	Mean	S.D.	Combined (All Lapita Mandibles) N	Mean	S.D.
MANDINDX	0			0			2	81.9	18.2
GONCONDX	0			0			2	82.7	7.1
RAMUSIND	1	67.2		0			5	66.0	9.4
ROBUST	1	34.5		1	41.4		9	39.9	7.2

[1]For explanation of abbreviations for mandibular measurements and indices see Pietrusewsky's Natunuku report (this volume).

Table 5. Summary of non-metric observations recorded in adult crania from Watom Island.

Trait	Watom n/N	%
Metopism absent	1/1	100.0
Frontal groove absent	2/2	100.0
Supraorbital structure single notch	1/1	100.0
Spina trochlea absent	2/2	100.0
Zygofacial foramen single	3/3	100.0
Nasal frontal suture omega	1/1	100.0
Subnasal blurred	1/1	100.0
Marginal tubercle none	1/1	100.0
Palatine torus none	1/1	100.0
Maxillary torus none	2/2	100.0
Parietal foramen single	1/1	100.0
Parietal notch none	1/1	100.0
Tympanic thickening present	1/1	100.0
Tympanic dehiscence absent	1/1	100.0
Tympanic marginal foramen absent	1/1	100.0
Auditory exostosis absent	1/1	100.0

Table 6. Summary of non-metric variation recorded in Lapita mandibles.

	Watom		Tonga		Lakeba		Manus		Natunuku	
Trait	n/N	%	n/N	%	n/N	%	n/N	%	n/N	%
Mandibular torus										
absent	6/6	100.0	2/2	100.0	2/2	100.0	2/2	100.0	2/2	100.0
Mylohyoid bridge										
no bridge	4/4	100.0	1/1	100.0	1/1	100.0			1/1	100.0
Multiple mandibular foramen										
absent	2/2	100.0	1/1	100.0	1/1	100.0			1/1	100.0
Multiple mental foramen										
absent	5/5	100.0	2/2	100.0	2/2	100.0	2/2	100.0	1/1	100.0
Rocker jaw										
none	1/4	25.0								
present	2/4	50.0								
partial anterior	1/4	25.0	1/1	100.0	2/2	100.0	1/1	100.0	1/1	100.0
Chin form										
median & angled inferiorly	2/4	50.0					1/1	100.0		
bilateral & angled inferiorly	1/4	25.0			2/2	100.0				
median, bilateral & angled inferiorly	1/4	25.0	1/1	100.0					1/1	100.0

Table 7. Descriptive statistics for tooth measurements, cross-sectional areas and tooth summary figures for Lapita dentitions (right & left sides combined).

	Watom			Tonga (Burial AK)			Natunuku			Manus			Combined		
Measurement	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.
UM3MD	3	8.0	0.8	0			0			0			3	8.0	0.8
UM3BL	3	10.3	0.8	0			0			0			3	10.3	0.8
UM2MD	4	10.2	1.0	0			1	10.1		0			5	10.2	0.9
UM2BL	4	11.7	0.4	0			1	12.3		0			5	11.9	0.4
UM1MD	3	10.3	0.3	0			0			0			3	10.3	0.3
UM1BL	3	12.0	0.5	0			0			0			3	12.0	0.5
UP4MD	3	6.1	0.6	0			0			0			3	6.1	0.6
UP4BL	3	9.5	0.6	0			0			0			3	9.5	0.6
UP3MD	3	6.4	0.7	0			0			0			3	6.4	0.7
UP3BL	3	9.7	0.3	0			0			0			3	9.7	0.3
UCMD	3	7.5	0.4	0			0			0			3	7.5	0.4
UCBL	3	8.5	0.2	0			0			0			3	8.5	0.2
ULIMD	3	6.7	0.7	0			0			0			3	6.7	0.7
ULIBL	3	6.6	0.7	0			0			0			3	6.6	0.7
UCIMD	3	8.7	0.1	1	7.4		0			0			4	8.4	0.7
UCIBL	3	7.1	0.5	1	7.9		0			0			4	7.3	0.6
UM3CX	3	81.6	8.1	0			0			0			3	81.6	8.1
UM2CX	4	120.5	13.3	0			1	124.2		0			5	121.3	11.7
UM1CX	3	122.8	3.0	0			0			0			3	122.8	3.0
UP4CX	3	57.6	2.1	0			0			0			3	57.6	2.1
UP3CX	3	62.3	4.8	0			0			0			3	62.3	4.8
UCCX	3	63.8	4.3	0			0			0			3	63.8	4.3
ULICX	3	44.7	8.6	0			0			0			3	44.7	8.6
UCICX	3	61.5	4.9	1	58.5		0			0			4	60.7	4.3
LM3MD	3	10.7	0.6	0			0			2	12.5	0.1	5	11.4	1.0
LM3BL	3	9.5	0.6	0			0			2	11.4	0.2	5	10.3	1.2
LM2MD	3	10.7	1.2	0			0			2	11.5	0.4	5	11.1	1.0
LM2BL	3	10.2	0.9	0			0			2	11.2	0.1	5	10.6	0.8
LM1MD	3	11.0	1.2	1	12.0		0			1	10.3		5	11.0	1.0
LM1BL	3	10.0	1.0	1	10.7		0			1	11.5		5	10.5	1.0
LP4MD	3	7.0	1.2	2	7.2	0.1	0			1	8.1		6	7.2	0.9
LP4BL	3	7.6	0.8	2	8.3	0.4	0			1	8.7		6	8.0	0.7
LP3MD	3	6.2	0.7	2	7.0	0.5	0			1	6.7		6	6.6	0.7
LP3BL	3	7.5	0.8	2	8.4	0.1	0			1	7.6		6	7.8	0.7
LCMD	3	6.3	0.3	2	6.8	0.2	2	6.9	0.6	2	7.0	0.4	9	6.7	0.4
LCBL	3	7.5	0.2	2	7.7	0.1	2	7.8	0.2	2	7.8	0.2	9	7.7	0.2
LLIMD	3	5.7	0.5	0			2	5.6	0.1	1	5.2		6	5.6	0.4
LLIBL	3	5.4	0.6	0			2	6.1	0.0	1	7.0		6	5.9	0.7
LCIMD	2	4.5	0.0	0			0			0			2	4.5	0.0
LCIBL	2	5.4	0.6	0			0			0			2	5.4	0.6
LM3CX	3	102.0	9.1	0			0			2	143.1	4.3	5	118.5	23.5
LM2CX	3	110.0	20.3	0			0			2	129.9	4.8	5	118.0	18.2
LM1CX	3	110.8	23.3	1	128.4		0			1	118.4		5	115.9	18.2
LP4CX	3	53.6	15.5	2	59.8	4.2	0			1	70.5		6	58.5	11.9
LP3CX	3	46.7	10.6	2	59.3	5.2	0			1	50.9		6	51.6	9.4
LCCX	3	47.0	1.9	2	53.1	1.2	2	54.2	5.9	2	55.4	4.3	9	51.8	4.6
LLICX	3	30.9	4.8	0			2	34.2	0.9	1	36.4		6	32.9	3.9
LCICX	2	24.3	2.5	0			0			0			2	24.3	2.5
TS	1	1140		0			0			0			1	1186	

Table 8. Incidence of dental non-metric traits recorded in male Lapita-associated dentitions.

	Watom		Tonga		Manus		Total	
Trait	n/N	%	n/N	%	n/N	%	n/N	%
Shovel-shaped incisors								
maxillary	5/6	83.3					5/6	83.3
mandibular	0/5	0.0					0/5	0.0
Peg-shaped								
teeth	0/53	0.0	0/9	0.0	0/11	0.0	0/73	0.0
Molar and premolar enamel extension								
absent	31/31	100.0	4/5	80.0	7/7	100.0	42/43	97.7
present			1/5	20.0			1/43	2.3
Protostylid cusp								
absent	11/12	91.7	1/1	100.0	6/6	100.0	18/19	94.7
present	1/12	8.3					1/19	5.3
Carabelli's cusp								
absent	10/10	100.0					10/10	100.0
present								
Maxillary molar cusp pattern								
M 3								
3	2/3	66.7					2/3	66.7
3+	1/3	33.3					1/3	33.3
M 2								
3+	1/2	50.0					1/2	50.0
4-	1/2	50.0					1/2	50.0
M 1								
3+	1/3	33.3					1/3	33.3
4	2/3	66.7					2/3	66.7
Mandibular molar cusp pattern								
M 3								
+4	2/3	66.7					2/3	66.7
Y4	1/3	33.3					1/3	33.3
M 2								
+4	4/4	100.0					4/4	100.0
M 1								
+4	1/2	50.0					1/2	50.0
Y5	1/2	50.0					1/2	50.0

Table 9. Incidence of premortem and postmortem tooth loss in Watom and other Lapita teeth.

	Watom		Tonga		Manus			
	Premortem		Premortem		Premortem		Postmortem	
Maxillary	n/N	%	n/N	%	n/N	%	n/N	%
M 3	1/4	25.0	–	–	–	–	–	–
M 2	0/3	0.0	1/1	100.0	–	–	–	–
M 1	0/4	0.0	0/1	0.0	–	–	–	–
P 4	0/3	0.0	0/2	0.0	–	–	–	–
P 3	0/3	0.0	0/2	0.0	–	–	–	–
C	0/3	0.0	0/2	0.0	–	–	–	–
I 2	0/3	0.0	0/2	0.0	–	–	–	–
I 1	0/3	0.0	0/2	0.0	–	–	–	–
Total M+P	1/17	5.9	1/6	16.7	–	–	–	–
Total C+I	0/9	0.0	0/6	0.0	–	–	–	–
Total	1/26	3.8	1/12	8.3	–	–	–	–
Mandibular								
M 3	0/4	0.0	2/2	100.0	0/1	0.0	0/1	0.0
M 2	0/4	0.0	2/2	100.0	0/2	0.0	0/2	0.0
M 1	0/4	0.0	1/2	50.0	0/2	0.0	0/2	0.0
P 4	0/4	0.0	0/2	0.0	0/1	0.0	0/1	0.0
P 3	1/4	25.0	0/2	0.0	1/1	100.0	0/1	0.0
C	1/4	25.0	0/2	0.0	0/1	0.0	1/1	100.0
I 2	1/4	25.0	1/1	100.0	0/2	0.0	1/2	50.0
I 1	2/4	50.0	–	–	0/2	0.0	2/2	100.0
Total M+P	1/20	5.0	5/10	50.0	1/7	14.3	0/7	0.0
Total C+I	4/12	33.3	1/3	33.3	0/5	0.0	4/5	80.0
Total	5/32	15.6	6/13	46.2	1/12	8.3	4/12	33.3

Table 10. Frequency of periodontal disease in Lapita-associated dental remains.

	Watom		Tonga		Manus		Total	
Trait	n/N	%	n/N	%	n/N	%	n/N	%
Calculus buildup								
absent					1/11	9.1	1/72	1.4
slight	34/52	65.4	9/9	100.0	5/11	45.5	48/72	66.7
moderate	17/52	32.7			5/11	45.5	22/72	30.5
marked	1/52	1.9					1/72	1.4
Resorption								
slight	3/48	6.3					3/69	4.3
moderate	39/48	81.3	15/15	100.0	6/6	100.0	60/69	87.0
marked	6/48	12.5					6/69	8.7
Rolled rim								
absent	2/41	4.9					2/41	4.9
slight	25/41	61.0					25/41	61.0
moderate	14/41	34.1					14/41	34.1

Table 11. Incidence of dental pathology in Lapita-associated dentitions.

	Watom		Tonga		Manus		Total	
Trait	n/N	%	n/N	%	n/N	%	n/N	%
Hypoplasia								
absent	50/52	96.2	9/9	100.0	11/11	100.0	70/72	97.2
slight	2/52	3.8					2/72	2.8
Caries								
absent	52/52	100.0	2/14	14.3	11/11	100.0	65/77	84.4
present			12/14	85.7			12/77	15.6
Abscessing								
absent	42/42	100.0	14/16	87.5	10/11	90.9	66/69	95.7
present			2/16	12.5	1/11	9.1	3/69	4.3
Attrition								
enamel	31/52	59.6					31/79	39.2
dentin	21/52	40.4	9/16	56.3	10/11	90.9	40/79	50.6
pulp			1/16	6.2			1/79	1.3
roots			6/16	37.5	1/11	9.1	7/79	8.9

Table 12. Descriptive statistics for measurements recorded in Lapita-associated infracranial skeletons from Watom Island.

	Left			Right		
Bone/Measurement	N	Mean	S.D.	N	Mean	S.D.
Clavicle						
Max. length	1	136.0		1	136.0	
Sag. diam. mid-shaft	3	11.0	1.0	3	11.7	1.5
Vertical (cranial-caudal) diam. (mid)	4	9.3	1.3	3	9.3	0.6
Circumference at mid-shaft	4	37.8	6.0	3	35.0	3.6
Humerus						
Max. length	2	337.5	17.5	1	303.0	
Max. head diam. (a-p)	2	45.0	1.4	1	42.0	
Min. head diam. (trans.)	2	40.5	3.5	1	37.0	
Epicondylar breadth	3	58.7	5.9	1	61.0	
Mid-circumference	3	70.0	4.4	3	71.3	3.5
Max. diam. mid-shaft	3	23.0	1.7	3	23.0	1.0
Min. diam. mid-shaft	3	18.7	1.2	3	19.0	1.0
Least circum. (distal to deltoid)	2	64.5	3.5	3	69.0	1.7
Radius						
Max. length	1	286.0		2	266.0	29.7
Radial head diam.	1	20.0		2	21.5	0.7
Sagittal diam. mid-shaft	3	11.0	1.0	3	11.7	1.5
Transverse diam. mid-shaft	3	14.0	1.0	3	16.3	1.5
Ulna						
Maximum length	1	305.0				
Dorso-volar diam. (max.)	2	16.5	0.7	2	17.5	2.1
Trans. diam. (perpend. to latter)	2	11.5	2.1	2	12.0	1.3
Min. circum. (near distal end)	2	33.0	2.8	2	36.0	1.4

Table 12 (cont'd).

Bone/Measurement	Left N	Left Mean	Left S.D.	Right N	Right Mean	Right S.D.
Femur						
Maximum length	1	452.0		1	466.0	
Bicondylar (physiological) length						
Epicondylar breadth	1	75.0		1	73.0	
Max. hd. diam.	2	44.0	4.2	3	44.0	3.5
Subtrochanteric (a-p) diam.	4	28.5	4.8	6	26.5	2.3
Subtrochanteric (trans.) diam.	4	33.0	6.7	6	29.8	2.1
Mid-shaft (a-p) diam.	4	29.0	3.9	6	29.7	2.4
Mid-shaft (trans.) diam.	4	24.3	2.6	6	25.0	1.3
Circum. mid-shaft	4	88.0	8.1	6	88.2	6.0
Tibia						
Max. length						
Max. epip. breadth-prox.						
Max. epip. breadth-distal						
Max. diam. at nutrient for.	2	32.5	0.7	2	33.5	3.5
Trans. diam. at nutrient for.	2	23.5	0.7	2	22.5	2.1
Circumference at nutrient for.	2	91.5	2.1	2	89.5	6.4
Mid-shaft a-p diam.	2	29.0	1.4	2	26.0	5.7
Mid-shaft trans. diam.	2	19.0	1.4	1	22.0	
Fibula						
Max. length	1	371.0				
Max. diam. at mid-shaft	1	42.0		1	46.0	
Patella						
Height	2	41.0	2.8	4	40.3	1.0
Width	4	40.5	1.0	4	41.3	2.4
Thickness	5	19.0	1.9	4	19.0	0.8
Calcaneus						
Max. length	2	76.5	3.5	3	78.3	1.2
Max. breadth	2	40.0	0.0	3	42.0	1.7
Talus						
Max. length	5	52.2	3.3	5	52.2	2.7
Max. breadth	4	39.8	1.9	5	39.4	2.7
Lumbar (ht. of centrum)		Post.			Ant.	
Lumbar 1.						
Lumbar 2.	1	26.0		1	23.0	
Lumbar 3.						
Lumbar 4.						
Lumbar 5.						

Table 13. Summary of estimated statures for Watom burials.

Burial No.	Sex	Age (yrs.)	Stature (cm.)	Stature (ft.,in)	Bone or segment length	Houghton *et al.* (1975) formula No.
1	F	30	164	5'5"	R. femur Seg.1 (7.7 cm)	1
2	F	19	154.7	5'1"	L. femur Seg.2 (21.1 cm)	7
3	M	30-40	176.2	5'9"	R. femur Seg.4 (3.9 cm)	1
4	M	35	170	5'7"	R. femur Seg.2 (23.5 cm)	1
5	M	30	173.7	5'8"	L. humerus (32.5 cm)	10
6	M	30-35	180	5'11"	L. humerus (35.0 cm)	10
7	M	Adult	172.7	5'8"	R. femur Seg.2 (24.8 cm)	1
8	M	Adult	171.9	5'7"	L. tibia Seg.3 (13.6 cm)	8

Table 14. Infracranial indices for Watom and Lapita male skeletal remains.

		Watom		Burial AK		Natunuku		Combined	
Index	Side:	L	R	L	R	L	R	L	R
Humeral robusticity	N/N	3/2 20.7	3/1 23.5					3/2 20.7	3/1 23.5
Humeral diaphyseal	N/N	3/3 81.3	3/3 82.6	1/1 95.2	1/1 90.5			4/4 84.4	5/5 85.7
Radio-humeral	N/N	1/2 84.7	2/1 87.8					1/2 84.7	2/1 87.8
Femur robusticity	N/N	4/1 11.8	6/1 11.7			1/1 12.5	1/1 12.8	6/2 12.1	7/2 12.1
Humeral-femur	N/N	2/1 74.7	1/1 65.0					2/1 74.7	1/1 65.0
Crural	N/N						1/1 88.7		1/1 88.7
Tibia-thickness	N/N	2/2 65.5	1/2 84.6	1/1 64.5		1/1 64.5	1/1 66.7	4/4 65.0	2/3 77.7
Platymeric	N/N	4/4 84.8	6/6 88.9	1/1 78.1		1/1 81.2	1/1 81.2	6/6 84.1	7/7 87.7
Pilastric	N/N	4/4 119.3	6/6 118.8	1/1 123.1		1/1 124.0	1/1 128.0	6/6 120.6	7/7 120.0
Platycnemic	N/N	2/2 72.3	2/2 67.2	1/1 61.1		1/1 67.6	1/1 63.9	4/4 68.0	3/3 66.2
Patella module	N/N	2-5 33.5	4 33.5		1 33.6			5-6 33.7	5 33.5

Table 15. Summary of non-metric traits recorded in the infracranial skeletons from Watom Island and Tonga (sides and sexes combined).

Trait and Variation	Watom n/N	Watom %	Burial AK n/N	Burial AK %	Total n/N	Total %
Clavicle						
Costoclavicular sulcus						
present	5/6	83.3	1/1	100.0	6/7	85.7
ridge	1/6	16.7			1/7	14.3
Supraclavicular foramen						
absent	5/7	71.4			5/7	71.4
present	2/8	28.6			2/7	28.6
Humerus						
Supratrochlear notch						
absent	4/4	100.0	2/2	100.0	6/6	100.0
Septal aperture						
absent	2/3	66.7	3/3	100.0	5/6	83.3
present	3/3	33.3			1/6	16.7
Ulna						
Trochlear notch shape						
indented	1/3	100.0	2/3	66.7	5/6	83.3
island			1/3	33.3	1/6	16.7
Innominate						
Acetabular notch						
absent	1/1	100.0			1/1	100.0
Pre-auricular sulcus GP						
absent	4/5	80.0			4/5	80.0
present	1/5	20.0			1/5	20.0
Pre-auricular sulcus GL						
absent	3/5	60.0			3/5	60.0
present	2/5	40.0			2/5	40.0
Femur						
Fossa of Allen						
absent	2/3	66.7			2/3	66.7
ulcer	1/3	33.3			1/3	33.3
Third trochanter						
ridge	3/3	100.0	1/1	100.0	4/4	100.0
Fovea capitis shape						
round	2/5	40.0			2/5	40.0
oval	3/5	60.0			3/5	60.0
Patella						
Vastus facet						
absent	2/12	16.7			3/14	21.4
present	10/12	83.3	1/1	100.0	11/14	78.6
Vastus notch						
absent	13/13	100.0	1/1	100.0	14/15	93.3
present					1/15	6.7
Patellar spurs						
absent	7/13	53.8	1/1	100.0	8/14	57.2
present	6/13	46.2			6/14	42.8
Tibia						
Anterior squatting facet						
present	2/2	100.0	1/1	100.0	3/3	100.0

Table 15 (cont'd).

Trait and Variation	Watom n/N	Watom %	Burial AK n/N	Burial AK %	Total n/N	Total %
Talus						
Talar extension						
absent			1/1	100.0	1/8	12.5
medial extension	5/7	71.4			5/8	62.5
med. & lat. ext.	2/7	28.6			2/8	25.0
Squatting facet						
absent	1/13	7.7			1/14	7.1
medial	2/13	15.4			2/14	14.3
neck	10/13	76.9			10/14	71.4
med. & lat. facet			1/1	100.0	1/14	7.1
Calcaneus						
Calcaneal facet						
two	5/9	55.6			5/9	55.6
hour-glass	4/9	44.4			4/9	44.4
Peroneal tubercle						
absent	3/5	60.0			3/5	60.0
present	2/5	40.0			2/5	40.0

Table 16. Summary of non-metric variation recorded in the vertebrae from Watom Island and Tonga (Burial AK) (sexes and sides combined).

	Watom		Burial AK		Total	
	n/N	%	n/N	%	n/N	%
Atlas Vertebra (C-1)						
Foramen transversarium						
normal	1/1	100.0			1/1	100.0
R:L foramen transversarium						
R > L	1/1	100.0			1/1	100.0
Bridging to sup. art. facet						
none or normal	8/8	100.0			8/8	100.0
Atlas bridging						
none or normal	8/8	100.0			8/8	100.0
Incomplete costal bar						
normal or complete	6/6	100.0			6/6	100.0
Spina bifida						
absent	2/2	100.0			2/2	100.0
Shape sup. articular facet						
single	2/8	25.0			2/8	25.0
constricted	6/8	75.0			6/8	75.0
Axis Vertebra (C-2)						
Apical process						
absent or normal	4/4	100.0	1/1	100.0	5/5	100.0
Foramen transversarium						
normal	2/2	100.0	1/1	100.0	3/3	100.0
Spina bifida						
none	2/2	100.0	1/1	100.0	3/3	100.0
Cervical Vertebrae 3-7						
Foramen transversarium						
normal	1/2	50.0	3/3	100.0	4/5	80.0
two	1/2	50.0			1/5	20.0
Spinous process						
none	1/1	100.0	1/1	100.0	2/2	100.0
Spina bifida						
none	4/4	100.0	1/1	100.0	5/5	100.0
Thoracic Vertebrae 1-12						
Laminal spurring						
absent	6/7	85.7			6/7	85.7
present	1/7	14.3			1/7	14.3
Spina bifida						
none	15/15	100.0			15/15	100.0
Lumbar Vertebrae 1-5						
Laminal spurring						
absent	5/5	100.0			5/5	100.0
Spina bifida						
none	10/10	100.0			10/10	100.0
Spondylolysis						
normal	5/5	100.0			5/5	100.0
Sacral Vertebrae						
Inferior sacral hiatus						
S-4/S-3	1/1	100.0			1/1	100.0

Table 17. Summary of incidence of osteoarthritis in the appendicular skeletons from Watom Island and Tonga (Burial AK) (right and left sides combined).

Articular Surface (Severity)	Watom n/N	Watom %	Burial AK n/N	Burial AK %	Total n/N	Total %
Sterno-clavicular						
none	3/3	100.0	1/1	100.0	4/4	100.0
Acromio-clavicular						
none	2/2	100.0			2/2	100.0
Glenoid cavity						
none	5/6	83.3			5/8	62.5
slight	1/6	16.7	2/2	100.0	3/8	37.5
Humeral head						
none	2/2	100.0			2/2	100.0
Capitulum						
none	6/6	100.0			6/8	75.0
slight			2/2	100.0	2/8	25.0
Trochlea						
none	7/7	100.0			7/9	77.8
slight			2/2	100.0	2/9	22.2
Radial head						
none	4/4	100.0			4/5	80.0
medium			1/1	100.0	1/5	20.0
Distal radius						
none	4/4	100.0			4/6	66.7
slight			2/2	100.0	2/6	33.3
Proximal ulna						
none	4/7	57.1			4/9	44.5
slight	3/7	42.9			3/9	33.3
medium			2/2	100.0	2/9	22.2
Distal ulna						
none	3/3	100.0	1/1	100.0	4/4	100.0
Sacroiliac joint						
slight	3/3	100.0	1/1	100.0	4/4	100.0
Acetabulum						
none	6/8	75.0			6/9	66.7
slight	2/8	25.0	1/1	100.0	3/9	33.3
Femoral head						
none	5/6	83.3	1/1	100.0	6/7	85.7
slight	1/6	16.7			1/7	14.3
Femoral condyles						
none	4/5	80.0			4/6	66.7
slight	1/5	20.0	1/1	100.0	2/6	33.3
Patella						
none	6/11	54.5			6/12	50.0
slight	5/11	45.5	1/1	100.0	6/12	50.0
Distal tibia						
none	2/3	66.7	1/2	50.0	3/5	60.0
slight	1/3	33.3	1/2	50.0	2/5	40.0

Table 17 (cont'd).

Articular Surface (Severity)	Watom n/N	Watom %	Burial AK n/N	Burial AK %	Total n/N	Total %
Proximal fibula						
none	1/1	100.0			1/1	100.0
Distal fibula						
none	4/4	100.0			4/5	80.0
slight			1/1	100.0	1/5	20.0
Calcaneus						
none	4/10	40.0			4/11	36.4
slight	6/10	60.0	1/1	100.0	7/11	63.6
Talus						
none	7/15	46.7			7/16	43.8
slight	8/15	53.3	1/1	100.0	9/16	56.2
Tarsals						
none	4/14	28.6	2/2	100.0	6/16	37.5
slight	10/14	71.4			10/16	62.5
Carpals						
none	7/11	63.6	1/2	50.0	8/13	61.5
slight	4/11	36.4	1/2	50.0	5/13	38.5
Metatarsals						
none	5/10	50.9			5/12	41.7
slight	5/10	50.0	2/2	100.0	7/12	58.3
Metacarpals						
none	6/12	50.0			6/14	42.9
slight	6/12	50.0	2/2	100.0	8/14	57.1
Hand phalanges						
none	10/12	83.3	2/2	100.0	12/14	85.7
slight	2/12	16.7			2/14	14.3
Foot phalanges						
none	8/10	80.0	2/2	100.0	10/12	83.3
slight	2/10	20.0			2/12	16.7

Table 18. Mandibular indices for Lapita and Asian-Pacific samples.

Group	Mandibular Index	Gonio-Condylar Index	Ramus Index
Watom	69.1	77.7	69.2
Lakeba	–	–	–
Burial AK	–	–	67.2
Manus	–	–	–
Natunuku	94.7	87.7	55.0
Combined Lapita	81.9	82.7	66.0
Fiji	94.0	83.9	57.6
Tonga	87.3	80.1	56.4
Namu	82.6	80.6	52.3
Wairau Bar	90.6	70.8	56.0
New Zealand	83.0	88.5	52.9
Society Is.	89.2	81.3	58.9
Marquesas	91.8	83.8	57.2
Easter Is.	86.1	79.2	63.8
Hawaii	85.7	82.7	54.0
E. Micronesia	94.7	87.0	57.5
Guam	88.7	85.1	58.2
Gulf of Papua	93.8	82.4	50.9
New Britain	90.6	83.0	54.8
New Ireland	92.0	81.5	53.0
New Caledonia	–	82.6	60.2
Loyalty	–	85.0	60.6
Vanuatu	–	80.4	54.9
China	–	83.6	55.9
South-east Asia	–	82.9	55.9
Thailand	–	82.7	53.4
Java	83.0	82.7	54.0
Sulu	–	83.2	54.6
Western Australia	–	83.4	53.5

Table 19. A comparison of non-metric variation in mandibles[1].

	Trait		
Sample	Mylo-hyoid bridge	Multiple mental foramen	Rocker jaw
Watom	0/4	0/2	3/4
	0.0	0.0	75.0
Lapita	0/7	0/5	8/9
	0.0	0.0	88.9
Polynesia	18/234	20/241	107/126
	7.7	8.3	89.2
Tonga	5/36	0/28	11/18
	13.9	0.0	61.1
Fiji	5/22	0/11	7/10
	22.7	0.0	70.0
E. Melanesia	9/173	22/191	52/94
	5.2	11.5	55.3
Bismarck Arch.	19/201	34/204	58/96
	9.4	16.7	60.4
Papua	1/165	13/160	74/78
	0.6	8.1	94.9
E. Asia	2/141	17/178	62/89
	1.4	9.6	69.7
S.E. Asia	4/112	9/114	35/52
	3.6	7.9	67.3
Island S.E. Asia	19/350	31/358	138/177
	5.4	8.7	78.0

[1]The comparative data are taken from Pietrusewsky (1977, 1984). The frequencies represent pooled information.

Table 20. A comparison of tooth summary figures for Lapita and selected Pacific and circum-Pacific samples.

	Tooth Summary Figure
China	1157
Watom Is.	1140
Lapita (combined)	1186
Chatham Island	1181
Borneo	1190
Hawaii	1200
Japan	1200
Marquesas	1204
Thailand	1233
Northern Marianas	1238
Java	1240
New Caledonia	1256
New Ireland	1266
North Coast Papua New Guinea	1286
Philippines	1288
Vanuatu	1295
Guam	1309
Samoa	1311
Sepik R.	1321
New Britain	1334
Fiji	1338
Bougainville	1359
Tonga	1371
Eastern Highlands Papua New Guinea	1395
Tasmania	1429
Murray River, Australia	1486

Table 21. A comparison of infracranial indices and stature for Lapita and Pacific Island male samples.

	Watom	Natunuku	Burial AK	Lapita	Fiji	Nebira	Tonga	Hawaii	New Zealand	Easter Island	Marquesas
Crural Index		88.7		88.7	84.2	84	83.5	84	82.4	83.7	82
Pilastric	119	124	123	120.6	133.7	121	116.9	115	116.7	115.8	122.2
Platymeric	84.8	81.2	78.1	84.1	94.5	82	84.8	71	65	72.7	76.5
Femoral robust.	11.8	12.5		12.1	13.1	13.5	12.6	14.6	12.4	12.0	13.3
Platycnemic	72/67*	67/64*	61	68	66.7	65	66.1	66		71.8	69.4
Humeral-femur	76/65*		74.4	72.5	70	70.3	72	71.8	71.2	72.9	
Stature	174	173	174		169	167	176	173	171	173	174

*Values are expressed for both sides: right/left.

Table 22. Means and standard deviations for 22 mandibular measurements for 7 male samples.

	Tonga (15)		Namu (16)		New Zealand (26)		Chatham Island (7)	
Measurement	Mean	S.D.	Mean	S.D	Mean	S.D.	Mean	S.D.
MANDLNTH	110.3	4.3	99.2	3.3	99.7	5.0	102.3	3.7
INFMANDL	64.8	5.9	63.8	4.0	64.1	5.2	65.3	4.4
ALVEOLGT	59.9	2.8	58.8	4.0	57.1	3.3	57.1	4.4
BICONDWH	123.5	8.5	120.8	3.0	123.4	8.4	127.1	5.6
MIDCONDW	105.1	6.4	102.1	2.2	102.7	7.6	102.1	5.7
BIGONIAL	99.0	7.2	97.6	4.6	103.5	5.8	112.6	5.0
BICANBTH	34.7	1.8	32.4	1.9	32.5	2.1	34.4	1.5
FRMOLBTH	64.9	2.8	61.9	3.6	59.6	3.4	62.3	2.8
THMOLBRH	73.6	3.3	71.1	3.9	68.6	3.9	72.4	3.5
SYMPHYHT	30.3	2.5	30.2	2.2	33.8	2.8	37.4	1.8
MENFORHT	30.3	3.0	30.3	2.3	32.8	2.6	36.0	1.7
CANINEHT	30.9	2.9	30.9	2.6	33.3	2.4	36.9	1.3
MOLARHT	28.5	3.6	28.3	2.6	31.9	3.1	32.3	2.1
SYMPHYBH	14.1	1.6	14.4	1.8	14.2	1.9	16.6	1.1
MENFORBH	11.7	0.8	10.9	1.8	12.3	1.7	12.9	0.7
CANINEBH	11.7	0.8	11.5	1.6	12.3	1.8	12.6	1.3
MOLARBTH	13.4	1.6	12.6	2.1	14.3	1.7	13.7	1.6
RAMUSHGT	63.2	7.8	68.2	5.9	68.5	5.9	71.6	2.1
RAMUSBTH	37.3	4.4	34.8	3.6	36.3	3.7	37.9	2.4
CONDYLGT	11.2	0.9	10.1	0.7	12.4	1.8	12.6	1.5
CONDBTH	21.5	2.1	22.6	1.3	23.5	1.9	24.7	2.6
MONETWO	20.9	1.4	23.2	1.3	20.8	1.9	20.7	1.5

	Wairau Bar (5)		Northern Marianas (10)		Lapita (7)	
Measurement	Mean	S.D.	Mean	S.D.	Mean	S.D.
MANDLNTH	113.4	4.5	108.3	3.7	98.1	5.0
INFMANDL	65.6	4.8	63.2	4.1	64.1	6.5
ALVEOLGT	58.4	4.2	60.5	4.2	60.3	7.5
BICONDWH	121.8	17.3	126.5	6.7	126.9	7.2
MIDCONDW	113.4	4.0	108.9	5.7	123.0	0.0
BIGONIAL	101.8	5.5	107.7	4.4	101.1	3.3
BICANBTH	33.0	1.4	34.4	2.6	33.7	2.1
FRMOLBTH	60.6	1.8	62.7	2.3	61.9	3.5
THMOLBTH	72.4	2.4	72.7	3.1	73.0	4.4
SYMPHYHT	35.2	2.3	33.2	1.8	29.1	3.3
MENFORHT	34.0	3.0	33.0	2.2	27.9	4.3
CANINEHT	35.6	2.9	33.8	1.6	28.6	3.6
MOLARHT	32.2	1.8	29.8	2.9	27.6	1.3
SYMPHYBH	14.4	1.1	15.4	1.3	13.9	1.5
MENFORBH	12.2	1.3	14.9	1.1	11.1	1.1
CANINEBH	12.0	1.2	13.8	1.2	11.4	1.0
MOLARBTH	14.8	0.8	15.3	1.4	13.7	1.1
RAMUSHGT	68.8	2.8	66.2	5.3	61.9	6.3
RAMUSBTH	39.0	1.6	38.0	2.4	38.9	5.0
CONDYLGT	11.8	2.4	11.3	0.8	10.9	0.4
CONDBTH	24.4	1.5	22.3	1.8	19.9	1.5
MONETWO	21.8	0.8	22.9	1.3	21.3	1.9

Table 23. A ranking of mandibular measurements for 7 male samples, according to F-values obtained in the final step of stepwise discriminant function analysis.

Step No.	Measurement	F-Value	d.f.B/d.f.W	P*
1	MANDLNTH	20.4	6/86	*
2	MIDCONDW	15.5	6/85	*
3	SYMPHYHT	13.8	6/84	*
4	BICONDWH	8.6	6/83	*
5	MENFORBH	6.0	6/82	*
6	MONETWO	5.5	6/81	*
7	CONDBTH	5.1	6/80	*
8	BIGONIAL	4.2	6/79	*
9	CONDYLGT	2.7	6/78	*
10	MOLARBTH	2.3	6/77	*
11	FRMOLBTH	1.9	6/76	NS
12	RAMUSBTH	2.2	6/75	NS
13	MOLARHT	1.7	6/74	NS
14	MENFORHT	3.1	6/73	*
15	SYMPHYBH	2.0	6/72	NS
16	RAMUSHBT	1.4	6/71	NS
17	THMOLBTH	1.2	6/70	NS
18	BICANBTH	1.0	6/69	NS
19	CANINEHT	0.7	6/68	NS
20	INFMANDL	0.6	6/67	NS
21	ALVEOLGT	0.4	6/66	NS
22	CANINEBH	0.6	6/65	NS

* = P<.01
NS = not significant

Table 24. Eigenvalues, percentage of total dispersion, cumulative percentage of dispersion and level of significance for the canonical variables.

Variable	Eigenvalue	% Dispersion	Cumulative % Dispersion	d.f.[1]	P[2]
I	4.59870	36.1	36.1	27	*
II	3.19327	24.9	61.0	25	*
III	2.19804	17.3	78.3	23	*
IV	1.26450	9.9	88.2	21	*
V	0.82056	6.4	94.6	19	*
VI	0.68878	5.4	100.0	17	*

[1] d.f.= degrees of freedom = (p+q-2) (p+q-4)...
[2] P <.01 when eigenvalues are tested for significance according to Bartlett's criterion: $\{N-1/2(p+q) \log_e(1+x)\}$, where N = total number of crania, p = number of variables, q= number of groups, x = eigenvalues, which are distributed approximately as chi-square (Rao, 1952:373).

Table 25. Canonical coefficients for mandibular measurements recorded in 7 male samples for the first 2 canonical variables arranged in decreasing order.

Canonical Variable I		Canonical Variable II	
Variable	Coefficient	Variable	Coefficient
CONDBTH	0.30736	MOLARBTH	0.32176
MIDCONDW	-0.18380	CONDYLGT	0.28552
RAMUSBTH	-0.12540	MONETWO	-0.28423
MANDLNTH	-0.11775	MOLARHT	0.25685
MENFORHT	0.11474	SYMPHYBH	-0.17818
SYMPHYHT	0.10116	MANDLNTH	-0.16665
MOLARHT	-0.07116	MIDCONDW	0.16531
CONDYLGT	0.06693	FRMOLBTH	-0.15845
RAMUSHGT	0.06197	SYMPHYHT	0.15420
CANINEBH	-0.05052	MENFORBH	-0.13438
BIGONIAL	0.04761	CANINEHT	-0.12143
ALVEOLGT	0.03799	CANINEBH	-0.11981
BICONDWH	0.03310	MENFORHT	-0.08260
BICANBTH	-0.03049	BIGONIAL	0.08234
MONETWO	-0.02651	BICONDWH	-0.07880
INFMANDL	-0.02285	RAMUSBTH	-0.07229
MENFORBH	0.02156	ALVEOLGT	0.06288
SYMPHYBH	0.02130	CONDBTH	-0.05067
THMOLBTH	-0.01193	THMOLBTH	0.04269
MOLARBTH	-0.00394	BICANBTH	0.02507
CANINEHT	0.00272	INFMANDL	-0.01547
FRMOLBTH	0.00203	RAMUSHGT	-0.00736

Table 26. Summary of classification results from stepwise discriminant function analysis for 7 male samples (number of cases classified in groups).

Group	NZ	TOG	CHT	NAM	NMR	WAI	LAP
New Zealand	24				1		
Tonga		14			1		
Chatham Island			7				
Namu				16			
Northern Marianas					10		
Wairau Bar	1					4	
Lapita							7
Total Cases Orig. Assign.	25	15	7	16	10	5	7
No. Cases Correctly Assign.	24	14	7	16	10	4	7
% Correct. Assign.	96	93.3	100	100	100	80	100

Table 27. Mahalanobis' generalised distances for 7 male samples using 6 mandibular measurements.

Group	NZ	TOG	CHT	NAM	NMR	WAI	LAP
New Zealand	–	10.879	2.612	5.939	11.238	20.958	28.758
Tonga		–	16.829	10.390	7.515	12.710	29.679
Chatham Is.			–	13.131	15.167	25.039	42.697
Namu				–	14.502	25.759	29.534
Northern Marianas					–	10.658	28.489
Wairau Bar						–	18.856
Lapita							–

Table 28. Means and standard deviations for 4 mandibular measurements for 8 male samples*.

		BIGONIAL		SYMPHYHT		RAMUSHGT		RAMUSBTH	
Group	(N)	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Polynesia	135	101.7	6.6	32.7	3.3	65.2	7.0	36.8	3.8
E. Melanesia	95	98.2	6.9	31.9	3.5	66.1	5.5	38.3	4.3
Is. S.E. Asia	50	98.7	5.7	32.3	2.5	63.3	5.5	34.3	2.3
S.E. Asia	93	100.5	6.4	32.2	3.0	63.9	5.6	34.7	3.2
E. Asia	38	100.3	6.0	34.2	4.9	62.3	4.9	34.7	2.1
Papua	30	95.0	4.9	30.1	3.8	62.8	8.0	32.2	2.4
Bismarck	46	97.5	6.4	30.8	3.8	66.2	6.0	36.1	3.5
Lapita	7	101.1	3.3	29.1	3.3	61.9	6.3	38.9	5.0

* The samples contain the following cranial series: Polynesia = Namu – 9, Tonga – 16, Tahiti – 14, Marquesas – 9, Easter Is. – 14, Chatham Is. – 10, New Zealand – 33, Hawaii – 30; E. Melanesia = Fiji – 9, Loyalty – 21, New Caledonia – 30, Vanuatu – 35; Is. South-east Asia = Java – 26, Sulu – 18, Philippines – 6; South-east Asia – Thailand – 59, Vietnam, Laos & Cambodia – 34; East Asia = China – 32, Japan – 6; Papua = Gulf – 12, Purari Delta – 9, Sepik R. – 9; Bismarck = New Ireland – 9, New Britain – 37; Lapita = Watom (Nos. 3,6, & M2) – 3, and one specimen each from Tonga, Manus, Natunuku, and Lakeba.

Table 29. A ranking of mandibular measurements for 8 male samples according to F-values obtained in the final step of stepwise discriminant function analysis.

Step No.	Measurement	F-Value	$d.f._B/d.f._W$	P*
1	RAMUSBTH	17.2	7/494	*
2	SYMPHYHT	7.9	7/493	*
3	BIGONIAL	4.9	7/492	*
4	RAMUSHGT	3.0	7/491	*

* $p < .01$.

Table 30. Eigenvalues, percentage of total dispersion, cumulative percentage of dispersion and level of significance for the canonical variables.

Variable	Eigenvalue	% Dispersion	Cumulative % Dispersion	d.f.[1]	P[2]
I	0.28943	59.3	59.3	10	*
II	0.14584	29.9	89.2	8	*
III	0.03638	7.5	96.7	6	*
IV	0.01618	3.3	100.0	4	*

[1] d.f. = degrees of freedom = (p+q-2) (p+q-4)...
[2] $P < .01$ when eigenvalues are tested for significance according to Barlett's criterion: $\{N-1/2(p+q)\log_e(1+x)\}$, where N = total number of crania, p = number of variables, q=number of groups, x = eigenvalues, which are distributed approximately as chi-square (Rao, 1952:373).

Table 31. Canonical coefficients for mandibular measurements recorded in 8 male samples for the first 2 canonical variables arranged in decreasing order.

Canonical Variable I		Canonical Variable II	
Variable	Coefficients	Variable	Coefficients
RAMUSBTH	0.28201	SYMPHYHT	0.16940
SYMPHYHT	-0.14056	BIGONIAL	0.10091
BIGONIAL	-0.03974	RAMUSBTH	0.09524
RAMUSHGT	0.03414	RAMUSHGT	-0.07294

Table 32. Summary of classification results from stepwise discriminant function analysis for 8 male samples (number of cases classified in groups).

Group	POLY	EMEL	ISEA	SEA	EA	PAP	BIS	LAP
Polynesia	30	7	4	10	33	18	15	18
E. Melanesia	6	37	3	5	6	11	17	10
Is. S.E. Asia	4	5	3	7	15	10	5	1
S.E. Asia	15	6	8	13	20	15	7	9
E. Asia	2	4	1	4	21	3	2	1
Papua	0	0	0	3	5	16	6	0
Bismarck	4	11	2	3	3	8	9	6
Lapita	1	1	0	0	0	1	0	4
Total Cases Orig. Assign.	135	95	50	93	38	30	46	7
No. Cases Correctly Assign.	30	37	3	13	21	16	9	4
% Correct Assign.	22.2	38.9	6.0	14.0	55.3	53.3	19.6	57.1

Table 33. Mahalanobis' generalised distances for 8 male samples using 4 mandibular measurements.

	Poly	E.Mel	Is.S.E.A.	S.E.A.	E.Asia	Papua	Bismark	Lapita
Polynesia	–	0.797	0.632	0.346	0.967	2.463	0.863	2.445
E.Melanesia		–	1.754	1.633	2.749	3.130	0.533	1.851
Is.S.E.Asia			–	0.103	0.484	0.850	0.981	4.149
S.E.Asia				–	0.569	1.777	0.954	3.513
E.Asia					–	2.391	2.487	5.441
Papua						–	1.315	5.616
Bismark							–	2.576
Lapita								–

Appendix C

Miscellaneous remains from Watom Island.

Explanation of information presented.

Year: The year the material was excavated, either 1966 or 1985.
Rectangle: The main Watom burials come from Rectangles I, III, IV at Site SAC(8).
Square: These apply only to the 1985 excavations and follow the scheme adopted by Green & Anson.
Notes: This refers to the information which accompanied the miscellaneous remains; for the most part it was copied verbatim from the information written on the bags containing these remains.
Bones: This is an inventory of the human dental and skeletal remains which were identified in each bag of miscellaneous material.
Animal: If animal remains were identified in these bags, they were noted here.
Cultural: Any cultural material identified in these remains was noted.
Data Collected: If any information, measurements or other observations, were made, they were entered here.
Assignment: If any of the human remains found among the miscellaneous material could be assigned to one of the eight major burials, it was noted here.
Comments: Any other observations regarding the miscellaneous remains were noted here.

Year: 1966
Rectangle: I
Square:
Notes: Misc. material from Burials 1, 2, ?4-leg bones.
Bones: Upper limb fragments and a plastic vial containing a single adult human (upper left?) canine.
Animal:
Cultural:
Data collected: Canine tooth: MD = 9.0 mm, BL = 9.1 mm, slight wear, no caries, calculus or hypoplasia.
Assignment: None.
Comments: Upper limb fragments too incomplete for further analysis.

Year: 1966
Rectangle: I
Square:
Notes: Misc. material from Burials 1, 2, ?4 – metatarsals, metacarpals, phalanges.
Bones: Left talus, left cuneiforms 1 and 3, left distal fibula fragment, right MT-1 and phalanges, right cuneiforms 1 and 2; probably from same Burial (No.1). Two right fifth metatarsals, two proximal phalanges for first metatarsal, two capitates.
Animal:
Cultural:
Data collected: Left talus L = 50 mm, L = 38 mm. A medial extension and slight osteoarthritic lipping is observed in the left talus.
Assignment: A majority of the bones can be assigned to Burial No. 1.
Comments:

Year: 1966
Rectangle: I
Square:
Notes: Misc. material from Burials 1, 2, ?4, ribs.
Bones: Four (adult human) rib fragments.
Animal:
Cultural:
Data collected: None.
Assignment: None.
Comments: Bone fragments were found to be individually wrapped in tissue paper and placed inside a small box, material had not been unwrapped prior to their study in 1987.

Year: 1966
Rectangle: I
Square:
Notes: Miscellaneous material from Burials 1, 2, ?4. Vertebrae, scapula, ulna.
Bones: Approximately 60 small fragments of mostly human bone including skull, long limb bones and ribs.
Animal: Some animal bone and coral fragments.
Cultural: Pieces of coral.
Data collected: None.
Assignment: None.

Comments: Remains found in a small box, too fragmentary for further analysis.

Year: 1985
Rectangle: I
Square:
Notes: Western two thirds to white sand.
Bones: Right talus(adult); fragment of first metatarsal.
Animal: Two pieces of shell.
Cultural:
Data collected: Talus: L = 55 mm, W = 41 mm; medial extension of trochlear surface, neck squatting facet and slight osteoarthritis observed in the talus.
Assignment: None.
Comments: Excavated by Green and Anson in 1985, completion of Specht's Trench 1 excavations.

Year: 1985
Rectangle: I
Square:
Notes: Lower levels (Specht).
Bones: Right patella fragment; left navicular fragment; fragment of right ischium (adult male?); left proximal ulna fragment; left second metacarpal fragment; left fifth metatarsal fragment; proximal hand phalanx; right trapezoid; 5 cranial fragments.
Animal: Some fragments of animal bone.
Cultural:
Data collected: Right patella – measurements: L = 40 mm, W = 42 mm, thickness = 19 mm; non-metric traits: vastus facet present, vastus notch absent, no patellar spurs.
Assignment: All, except ischium and left proximal ulna fragments and right trapezoid, are assigned to Burial 1.
Comments: Excavated by Green and Anson in 1985, completing Specht's work.

Year: 1985
Rectangle: I
Square: E11
Notes:
Bones: None.
Animal: Two major unidentified non-human bone fragments.
Cultural:
Data collected:
Assignment:
Comments:

Year: 1985
Rectangle: I
Square: F10
Notes: Feature Y.
Bones: None.
Animal: Fragment of spinous process of a thoracic vertebra and (?pig) canine.
Cultural:
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: I
Square: G11
Notes: Feature 3.
Bones: Distal phalanx of first metatarsal; left metacarpal-4; 3 toe phalanges; metacarpal fragment, cranial fragments.
Animal:
Cultural:
Data collected:
Assignment: Distal phalanx and left fourth metacarpal probably belong to Burial 5.
Comments:

Year: 1985
Rectangle: I
Square: H11
Notes: Burial 2(?)
Bones: Right fibula fragment; left and right tibia fragments; right calcaneus fragment; small fibula and tibia

fragments.
Animal:
Cultural:
Data collected: Left tibia metrics: mid-shaft A-P = 27 mm, trans.= 20 mm, mid-circum = 74 mm; right tibia metrics: mid-shaft A-P = 27 mm, trans.= 21 mm, circum = 77 mm. Squatting facet present in right tibia.
Assignment: Not Burial 2, the two tibia fragments probably go with Burial 1, a small individual (female?).
Comments:

Year: 1985
Rectangle: III
Square: E13
Notes:
Bones: Fragment of left zygoma; middle hand phalanx and many minute bone fragments.
Animal:
Cultural:
Data collected: None.
Assignment:
Comments: Material too fragmentary for further analysis.

Year: 1985
Rectangle: III
Square: F12
Notes:
Bones: Proximal hand phalanx and 3 (human?) bone fragments.
Animal:
Cultural:
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: III
Square: F12
Notes: Feature 1.
Bones: Left talus.
Animal: Two pieces of shell/coral.
Cultural:
Data collected: Talus: L = 49 mm, medial extension, neck squatting facet, no arthritic lipping.
Assignment: Talus probably belongs to Burial 3.
Comments:

Year: 1985
Rectangle: III
Square: F13
Notes:
Bones: Five fragments of human bone.
Animal: One fragment of animal bone and one non-human tooth.
Cultural:
Data collected: None.
Assignment: None.
Comments: Material too fragmentary for futher analysis.

Year: 1985
Rectangle: III
Square: F13
Notes:
Bones: Distal fragment of large right humerus.
Animal:
Cultural:
Data collected: Size indicates male.
Assignment: Humerus fragment probably belongs to Burial 5.
Comments:

Year: 1985
Rectangle: III
Square: F14
Notes:

Bones: A few fragments which may be human, but majority are non-human.
Animal: Animal tooth and fragments of animal bone.
Cultural:
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: III
Square: F and G 12
Notes:
Bones: Unidentified human (?) bone fragments.
Animal: None.
Cultural:
Data collected: None.
Assignment: None.
Comments: Material is too fragmentary to allow further analysis. Some stones identified.

Year: 1985
Rectangle: III
Square: H12
Notes:
Bones: Fragments of scapula, limb bone and upper (right?) central incisor.
Animal: Animal tooth and bone fragments, pieces of coral.
Cultural:
Data collected: Upper right central incisor, measurements: MD = 8.9 mm, BL = 7.5 mm; pathology: calculus = ++, no caries nor hypoplasia. Shovel-shaped condition indeterminate.
Assignment: None.
Comments:

Year: 1985
Rectangle: III
Square: H15
Notes:
Bones: Two small (human?) bone fragments.
Animal:
Cultural:
Data collected: None.
Assignment: None.
Comments: Material too fragmentary for further analysis.

Year: 1985
Rectangle: III
Square: I12
Notes:
Bones: 15 bone fragments.
Animal:
Cultural:
Data collected: None.
Assignment: None.
Comments: Material is too fragmentary for further analysis.

Year: 1985
Rectangle: III
Square: I12/I13
Notes:
Bones: Adult right fifth metatarsal missing distal end; adult left third metatarsal (no head); 6 bone fragments.
Animal:
Cultural:
Data collected:
Assignment: Metatarsal fragments probably from Burial 2.
Comments:

Year: 1985
Rectangle: III
Square: I13
Notes:

Bones: None.
Animal: Most of material is non-human.
Cultural:
Data collected:
Assignment:
Comments:

Year: 1985
Rectangle: III
Square: I13
Notes:
Bones: One small (unidentified) human bone fragment.
Animal: Animal bone.
Cultural: A potsherd.
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: III
Square: I15
Notes:
Bones: Approximately 13 human bone fragments.
Animal: Several animal (turtle?) bone fragments.
Cultural:
Data collected: None.
Assignment: None.
Comments: Material too fragmentary for further analysis.

Year: 1985
Rectangle: IV
Square: J10
Notes:
Bones: Human rib and cranial fragments, (first?) molar.
Animal: Large metatarsal and other fragments of animal bone.
Cultural:
Data collected: None.
Assignment: None.
Comments: Material too fragmentary for further identification.

Year: 1985
Rectangle: IV
Square: J10
Notes:
Bones: Fragments of vertebrae; coracoid process (left?); 5 foot phalanges; left third metatarsal fragment; right fifth metacarpal; fragment of left ulna shaft; a single molar.
Animal:
Cultural:
Data collected: Moderate (++) wear on molar.
Assignment: Ulna and left MT-3 assigned to Burial 8; rest of material probably belongs to Burials 7 or 8.
Comments:

Year: 1985
Rectangle: IV
Square: J11
Notes:
Bones: Left talus fragment; right navicular fragment; left third cuneiform; 4 hand phalanges; 2 metacarpal fragments; 7 vertebrae (cervical and lumbar) fragments; rib and various limb bone fragments; 5 fibula fragments; adult premolar tooth.
Animal:
Cultural:
Data collected: Left talus measurements: L = 51 mm, B = 37 mm.
Assignment: Left talus fragment and left cuneiform assigned to Burial 7; right navicular and fibula fragments may go with either Burials 7 or 4.
Comments:

Year: 1985
Rectangle: IV
Square: J11
Notes:
Bones: Right distal humerus fragment; hand (middle) phalanx.
Animal:
Cultural:
Data collected: None.
Assignment: All material from Burial 7 or 8.
Comments:

Year: 1985
Rectangle: IV
Square: J11
Notes:
Bones: Fragments of two phalanges; right lower canine; several unidentified bone fragments.
Animal:
Cultural:
Data collected: Canine tooth: MD = 7.3 mm, BL = 8.2 mm; no caries or hypoplasia; moderate (++) wear.
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: J11
Notes:
Bones: Right third metacarpal fragment, proximal end of left fifth metacarpal; proximal hand phalanx; 4 unidentified human bone fragments.
Animal: Three non-human bone fragments.
Cultural:
Data collected: None.
Assignment: Right third metacarpal and left fifth metacarpal probably belong to Burial 8.
Comments:

Year: 1985
Rectangle: IV
Square: J11
Notes: ?Burial 4
Bones: Right humerus missing head region; cervical vertebrae 1 and 2; many rib fragments, left fifth metatarsal fragment; clavicle fragment; upper right premolar.
Animal:
Cultural:
Data collected: Humerus: mid-circum. = 73 mm, max head diam. = 25 mm, min hd. diam. = 20 mm.
Assignment: Humerus and clavicle belong to Burial 7 or 8; fifth matatarsal assigned to Burial 8.
Comments:

Year: 1985
Rectangle: IV
Square: J12
Notes:
Bones: Small fragment of clavicle.
Animal:
Cultural:
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: J12
Notes:
Bones: One possible scapula fragment.
Animal: Most of this material is non-human.
Cultural:
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: J12
Notes:
Bones: Large rib fragment, very large (left?) scaphoid fragment; large (left?) second metacarpal; proximal hand phalanx fragment; thoracic vertebra fragment; right second metatarsal; distal end of right ulna.
Animal: Some.
Cultural:
Data collected: None.
Assignment: Scaphoid, second metacarpal and proximal hand phalanx are probably from same individual (either Burial 7 or 8). Ulna fragment may belong to Burial 8 or 4.
Comments:

Year: 1985
Rectangle: IV
Square: J13
Notes:
Bones: Spine of a thoracic vertebra.
Animal:
Cultural:
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: J13
Notes:
Bones: None.
Animal: Some.
Cultural:
Data collected:
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: J13
Notes:
Bones: Three vertebrae (cervical) fragments; rib fragment; adult molar (lower right first molar).
Animal:
Cultural:
Data collected: Moderate (++) lipping on centra of lower cervical vertebrae; molar measurements: BL = 11.2 mm, MD = 12.8 mm, dental non-metric traits: slight (+) attrition, no caries, hypoplasia nor enamel extension.
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: J-K10
Notes: Feature marked (e) identified as a human rib fragment.
Bones: Rib fragment.
Animal:
Cultural:
Data collected: None.
Assignment: None.
Comments: Because of the large size and appearance of this fragment, its identification as human is in question.

Year: 1985
Rectangle: IV
Square: K10
Notes:
Bones: Three lower limb fragments.
Animal: Two rib fragments of (?) animal.
Cultural:
Data collected: None.

Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: K10
Notes:
Bones: Numerous limb bone fragments, (right?) scapula fragment; large right femur fragment.
Animal:
Cultural:
Data collected: Right femur fragment: sub-trochanteric A-P = 29 mm, Tran. = 25 mm; mid-shaft A-P = 31 mm, Tran. = 24; mid-shaft circum. = 82 mm.
Assignment: Scapula and femur fragment probably are from Burial 8.
Comments:

Year: 1985
Rectangle: IV
Square: K10
Notes: Grey sand midden layer, Spit...June 12, 1985. Fragment of human jaw – "rocker type", from left side.
Bones: Fragment of left mandible, condyle fragment from left side of same mandible; mandibular left first molar.
Animal: Animal tooth.
Cultural:
Data collected: Measurements and non-metric traits recorded in mandible and teeth as Mandible 1.
Assignment: Mandible 1 not associated with numbered burials from site.
Comments: Adult male (not young).

Year: 1985
Rectangle: IV
Square: K10
Notes:
Bones: Small forearm bone fragment and other small fragments.
Animal: Large number of fragments.
Cultural:
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: K10
Notes:
Bones: Thoracic spine fragment; left lunate; scapula and rib fragments; mid-shaft fragment of radius; right first cuneiform; right talus fragment; 2 teeth (upper? left second molar, lower? right second premolar).
Animal: Some non-human bones and coral debris.
Cultural:
Data collected: Left lunate: no arthritis; right first cuneiform: slight osteoarthritis; right talus: slight osteoarthritis.
Assignment: Cuneiform and fragment of right talus probably belong to Burial 4; left lunate may belong to Burials 4, 7 or 8.
Comments:

Year: 1985
Rectangle: IV
Square: K11
Notes:
Bones: Eight small human (limb) bone fragments, a lower (left?) first molar.
Animal: None.
Cultural:
Data collected: Human molar: MD = 11.2 mm, BL = 11.5 mm; moderate (++) wear, no caries.
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: K11
Notes: Black loan layer. Spit 3. Base of deposit. Human skull bones.

Bones: Cranial fragments which were reconstructed to give a relatively complete occipital bone, left zygoma and portion of temporal bone with mastoid process. At least fourteen more cranial fragments and four limb bone fragments were identified.
Animal:
Cultural:
Data collected: Occipital metrics: thickness recorded at lambda (= 12 mm), left asterion(= 10 mm), right asterion (= 11 mm). Cheek height of left zygoma = 26 mm, breadth of mastoid process = 21 mm. There is ridge and slight inion development in the occipital bone.
Assignment: None.
Comments: Material appears to represent one individual, a large male.

Year: 1985
Rectangle: IV
Square: K11
Notes:
Bones: Metatarsals 2, 3, & 5 from right side; distal half of left(?) humerus; distal end of right humerus, fragment (coracoid process) of right scapula.
Animal:
Cultural:
Data collected: None.
Assignment: All, except metatarsals, may belong to Burial 7 or 8. The metatarsals appear to represent a single individual.
Comments:

Year: 1985
Rectangle: IV
Square: K11
Notes:
Bones: None.
Animal: Mostly non-human remains.
Cultural:
Data collected:
Assignment:
Comments:

Year: 1985
Rectangle: IV
Square: K11
Notes:
Bones: Fragment of left patella; proximal fragment of left second metatarsal; matacarpal fragment; several other fragments.
Animal: Some.
Cultural: Pot sherd fragment (red in colour).
Data collected: Left patella Ht. = 18 mm; patellar spurs, vastus facet but no vastus notch, no osteoarthritis; metatarsal fragment exhibits little or no osteoarthritis.
Assignment: Left patella fragment probably belongs to Burial 4; metatarsal fragment may go with either Burials 7 or 8.
Comments:

Year: 1985
Rectangle: IV
Square: K-12
Notes: Grey sand midden layer spit 1:0-10 cm. June 11, 1985. Human jaw and skull fragment associated with big stone high up in pit. Rocker type.
Bones: Left side of mandible with in-tact dentition.
Animal:
Cultural:
Data collected: All material recorded as Mandible 2.
Assignment: Mandible 2.
Comments: Not as large as Mandible 1 but probably male.

Year: 1985
Rectangle: IV
Square: K12
Notes:
Bones: Left fourth metatarsal fragment; large proximal phalanx of first metatarsal; many limb bone fragments.

Animal: Two non-human teeth and non-human bones and bone fragments.
Cultural:
Data collected: None.
Assignment: Foot bones probably from same individual (Burial 8).
Comments:

Year: 1985
Rectangle: IV
Square: K12
Notes:
Bones: Large fragment of right scapula (adult) which preserves a portion of the glenoid cavity, spinous process and adjoining area; upper left adult canine; fragments of rib, vertebrae, metacarpals etc. totalling approximately 38 items.
Animal: Some fragments of animal bone.
Cultural:
Data collected: Glenoid cavity of scapula fragment is free of osteoarthritis.
Canine: Attrition exposes dentin, no caries or hypoplasia observed.
Assignment: Scapula fragment probably goes with Burial 8.
Comments:

Year: 1985
Rectangle: IV
Square: K12
Notes:
Bones: Vertebrae fragments (cervical and thoracic); large right second metacarpal fragment; middle hand phalanx; fragment of maxillary third molar and a complete maxillary right third molar.
Animal:
Cultural:
Data collected: Complete maxillary right third molar; moderate expressions of calculus and attrition, no caries.
Assignment: Large right second metacarpal may belong to Burial 7 or 8.
Comments:

Year: 1985
Rectangle: IV
Square: K13
Notes:
Bones: Several small bone fragments.
Animal:
Cultural:
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: K13
Notes: Feature marked (i).
Bones: Two rib fragments and a spinous process of one thoracic vertebra.
Animal:
Cultural:
Data collected: None.
Assignment: None.
Comments:

Year: 1985
Rectangle: IV
Square: Clean-up of all squares.
Notes:
Bones: Fragments of right (adult) patella; middle hand phalanx; more than three limb bone fragments; 16 unidentified bone fragments.
Animal: Some animal bone fragments.
Cultural:
Data collected: Patella measurements: B = 37 mm, W = 19 mm; no vastus notch and no patellar spurring.
Assignment: Patella probably goes with Burial 8.
Comments:

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Dentition of Watom Island, Bismarck Archipelago, Melanesia

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ABSTRACT. Teeth belonging to two adults excavated from the Lapita level occupation of Watom Island (ca. 2,300 years before present [YBP]) are described and compared with three large dental series from New Britain, recent Thailand, and Mokapu, Hawaii. As far as can be determined from a sample of two individuals, the Watom teeth appear to be more like those from New Britain than Thailand or Hawaii. All teeth are free of dental caries, hinting that the Watom diet was not overly dependent on sticky carbohydrate foodstuffs.

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The current anthropological view about the origin of Polynesians recognises a link between a pottery type called Lapita ware and the first settlements in Polynesia (Howells, 1973; Green, 1979; Bellwood, 1979). This ceramic type has been found in several archaeological sites in Melanesia, suggesting that Polynesians originated from the Melanesian gene pool. However, various physical anthropological studies have shown that Polynesian skeletal and dental features are more like those of south-east Asians than Melanesians. Until recently there have been no studies on human skeletal remains found in association with Lapita ceramics. Even now, such studies are limited to a few fragmentary skeletons (Pietrusewsky, 1985, n.d.; Kirch, Swindler & Turner, 1989). Therefore, even small amounts of information are valuable in attempting to reconstruct the biological characteristics of the Lapita ware people.

Dental anthropology is proving to be a powerful adjunctive resource for biohistoric research. This is because dental features such as incisor shovelling, cusp numbers and groove patterns are evolutionarily stable due to their polygenic inheritance. Even in very small populations, genetic drift has only a minimal effect, and major environmental shifts have almost no identifiable selective effect in blocks of time involving less than 5,000 years.

Given the theoretical importance of the Lapita-first Polynesian correspondence, and the methodological power of dental anthropology, a lengthy description of the Watom dentition is warranted.

Materials and Methods

The dentitions described and compared herein originated from 8 km wide Watom Island, located about 8 km offshore of New Britain's northern Gazelle Peninsula

Table 1. Watom Dental Morphology.

Maxilla	No. 3 R	No. 3 L	No. 6 R	No. 6 L
I1 Winging	3	3	3	3
I1 Shovel	1		1	1
I2 Shovel	1		1	1
I1 Double-shovel	0		1	0
I2 Double-shovel	0		0	0
I1 Interrup.groove	0		0	0
I2 Interrup.groove	0		0	0
I1 Tuberculum dent.	0		0	0
I2 Tuberculum dent.	0		0	1
C Mesial ridge			0	0
P1 Mes./dist. cusps			0	0
P2 Mes./dist. cusps			0	0
P1 Uto-Aztec	0		0	0
M1 Metacone	5		5	5
M2 Metacone	5	5	4	4
M3 Metacone		3.5	3.5	3.5
M1 Hypocone	4		4	4
M2 Hypocone	3.5	3.5		2
M3 Hypocone		0	0	0
M1 Cusp 5			0	0
M2 Cusp 5	0	2		0
M3 Cusp 5		0	0	0
M1 Carabelli				
M2 Carabelli	0			0
M3 Carabelli		0	0	0
M1 Parastyle	0		0	0
M2 Parastyle	0	0		0
M3 Parastyle		0	0	0
Mandible				
I1 Shovel			0	0
P1 Lingual cusp form			A	A
P2 Lingual cusp form	3	3	A	A
M1 Groove pattern	Y	Y	Y	Y
M2 Groove pattern	+	X	+	+
M3 Groove pattern	X	X	X	X
M1 Cusp number			5	5
M2 Cusp number	>4	>4	4	4
M3 Cusp number	4	5	5	5
M1 Deflect. wrinkle				
M2 Deflect. wrinkle				0
M3 Deflect. wrinkle	0	0	0	0
M1 C1-C2 crest				
M2 C1-C2 crest	0	0	0	0
M3 C1-C2 crest	0	0	0	0
M1 Protostylid	0	0	0	0
M2 Protostylid	0	0	0	0
M3 Protostylid	0	0	0	0
M1 Cusp 5				
M2 Cusp 5			0	0
M3 Cusp 5	0	5	3	3
M1 Cusp 6			0	0
M2 Cusp 6			0	0
M3 Cusp 6	0	0	0	0
M1 Cusp 7	0	0	0	0
M2 Cusp 7	0	0	0	0
M3 Cusp 7	0	0	0	0

	No. 3 R	No. 3 L	No. 6 R	No. 6 L
P1 Enamel extension	0		0	0
P2 Enamel extension	0		0	0
M1 Enamel extension	0		0	0
M2 Enamel extension	0	0		0
M3 Enamel extension		0	0	0
I1 Root number	1		1	1
I2 Root number				
C Root number			1	1
P1 Root number	2		1	
P2 Root number				
M1 Root number	3		3	3
M2 Root number	3	3		3
M3 Root number		1	1	
I1 Radical number				
I2 Radical number				
C Radical number			2	
P1 Radical number				
P2 Radical number				
M1 Radical number			7	
M2 Radical number				
M3 Radical number			4	
I2 Peg/reduced	0		R	R
I2 Congenital absent	0	0	0	0
M3 Peg/reduced	0	0	0	0
M3 Congenital absent	0	0	0	0
P2 Congenital absent	0	0	0	0
P1 Odontome				0
P2 Odontome			0	0
P1 Enamel extension		0	0	0
P2 Enamel extension	0	0	0	0
M1 Enamel extension	0	0	0	0
M2 Enamel extension	0	0	1	0
M3 Enamel extension	0	0	0	0
I1 Root number		1		
I2 Root number		1		
C Root number	1	1		
P1 Root number	1	1		
P2 Root number				
M1 Root number	2	2	2	2
M2 Root number	2		2	2
M3 Root number				
I1 Radical number				
I2 Radical number				
C Radical number				
P1 Radical number		2		
M1 Radical number				
M2 Radical number				
M3 Radical number				
P1 Tomes root		0		
P1 Odontome			0	0
P2 Odontome			0	0
I1 Congenital absent	0	0	0	0
P2 Congenital absent	0	0	0	0
M3 Congenital absent	0	0	0	0
M3 Torsomolar angle			0	0

(ca. 4°S, 152°E). The skeleton from burial 3 was excavated by J. Specht (1968), and that from burial 6 by R.C. Green & D. Anson (1987). Their antiquity is about 2,100 to 2,500 YBP. Other aspects of these skeletons have been studied by P. Houghton & M. Pietrusewsky (this volume).

All of the 64 possible teeth were preserved. They are moderately worn suggesting young to middle-aged adults at time of death. The very large teeth of skeleton 3 suggests a male, the slightly smaller teeth of skeleton 6 are less definitive, but possibly a male also. The amount of tooth wear points to both individuals having been about 30 to 50 years old at the time of their deaths. Neither individual had any dental caries, antemortem tooth loss, or alveolar abscessing, but periodontal disease was severe in 3 and medium in 6 (ranking defined in Turner, 1979). The absence of caries and the presence of moderate to severe periodontal disease is much more often the oral health signature of hunting, gathering and fishing economies than those based on agriculture with its cariogenic sticky carbohydrate foodstuffs (Turner, 1979).

While neither individual had any tooth modification such as filing, incising or intentional staining, the labial surfaces of the upper and lower incisors of skeleton 6 evidenced fine horizontal polishing striations and cleaning. There are no interproximal toothpick grooves. Perhaps both individuals practiced some form of oral hygiene since tartar accumulations were minor. Tartar deposits are often heavy in agricultural populations.

Neither individual has a rocker jaw, although 6 has what I refer to as 'almost' rocker.

Dental Morphology

Table 1 lists all of the major dental variants identifiable in each individual. The scoring of these variants and expression follow the ASU dental anthropology system (Turner, 1979; n.d.a). Table 2 compares the 16 most important traits in Watom, Mokapu, recent Thai and New Britain teeth. Comparing frequencies, Watom is most like the Thai for two traits, most like Mokapu for four traits, and most like New Britain for nine traits.

Table 3 provides multivariate inter-group Mean Measures of Divergence values based on the values in Table 2. The various negative MMDs are not statistically significant, whereas the positive values are. Although this MMD comparison fails to identify which group is most

Table 2. Key dental traits in Watom and comparative series.

Trait	Dichotomisation		Watom	Mokapu	Recent Thai	New Britain
UI1	Winging (1/1-4)	%	0.0	22.9	28.6	25.0
		n	(0/2)	(38/166)	(20/70)	(28/112)
UI1	Shovel (3-6/0-6)	%	0.0	23.5	31.1	9.3
		n	(0/2)	(39/166)	(23/74)	(10/108)
UI1	Double-shovel (+/0,+)	%	0.0	26.3	25.4	3.7
		n	(0/2)	(45/171)	(15/59)	(4/107)
UM2	Hypocone (2-5/0-5)	%	100.0	93.3	89.7	92.7
		n	(2/2)	(182/195)	(96/107)	(166/179)
UM3	Parastyle (1-4/0-4)	%	0.0	5.2	5.2	5.7
		n	(0/2)	(6/115)	(4/77)	(7/123)
UM1	Enamel ext. (2-3/0-3)	%	0.0	20.5	35.8	4.7
		n	(0/2)	(42/205)	(39/109)	(7/150)
UP1	One root (1/1-3)	%	50.0	60.8	67.3	48.8
		n	(1/2)	(104/171)	(72/107)	(61/125)
UM2	Three roots (3-4/1-4)	%	100.0	45.8	80.9	86.3
		n	(2/2)	(76/166)	(72/89)	(120/139)
UM3	Peg/reduce/cong.abs. (PRC/normal,PRC)	%	0.0	(34.5)	(18.7)	(16.7)
		n	(0/2)	(69/200)	(24/128)	(26/156)
LP2	>1 lingual cusp (2-3/1-3)	%	50.0	82.9	73.7	91.5
		n	(1/2)	(150/181)	(73/99)	(140/153)
LM2	Y groove pattern (Y/Y,+,X)	%	0.0	15.0	19.1	25.4
		n	(0/2)	(28/186)	(21/110)	(46/181)
LM2	Four cusps (4/4-6)	%	50.0	35.2	19.0	51.8
		n	(1/2)	(62/176)	(19/100)	(88/170)
LM1	Protostylid (1-7/0-7)	%	0.0	16.3	26.8	21.2
		n	(0/2)	(30/184)	(26/97)	(40/189)
LM1	Cusp 7 (1-4/0-4)	%	0.0	7.9	3.8	13.0
		n	(0/2)	(15/190)	(4/104)	(25/192)
LM1	Three roots (3/1-3)	%	0.0	12.0	11.3	4.5
		n	(0/2)	(22/184)	(15/133)	(7/155)
LM2	One root (1/1-3)	%	0.0	30.0	28.7	2.0
		n	(0/2)	(51/170)	(37/129)	(3/149)

U denotes upper jaw; L, lower jaw

Table 3. Mean measures of divergence.

	Mokapu	Recent Thai	New Britian
Watom	-.064	-.116	-.124
Mokapu		.056	.172
Recent Thai			.185

similar to Watom, it is evident that Mokapu dentition is almost three times more like that of the Thai than like New Britain teeth.

Finally, we can ask what is the probability of obtaining the trait frequencies listed for each group in Table 1. The probabilities will be the product of multiplying the frequencies of each trait in a group. Reciprocals are used for all groups where Watom trait frequencies are zero. The probability of getting exactly the Mokapu trait frequencies is 0.0066; Thai, 0.0045; New Britain, 0.0434; and Watom, 0.125. Comparing these probability values, we see that Watom is more similar to New Britain than Mokapu or Thailand.

The dentitions of the two Watom crania are more similar to teeth from New Britain than to teeth of recent Thai or late prehistoric Hawaiians. Insofar as a sample of two individuals can be trusted to represent a population, the Watom dentition suggest that the Lapita wares found on this small island were associated with Melanesians. Given the nearness of Watom to New Britain, this finding is reassuring in the sense that we would expect Watom teeth to be most like those of the larger and more heavily populated New Britain. Only on small islands far away from larger ones might we expect to find Lapita ceramics associated with non-Melanesian dentitions and skeletal features if Lapita and ancestral Polynesians were moving rapidly out of South-east Asia into Melanesia. Such seems to have happened on the northern edge of the Bismarck Archipelago where a small sample of teeth from the Mussau Islands is slightly more like teeth of South-east Asia than Melanesia (Kirch, Swindler & Turner, 1989). Finally, if one chooses to accept the small Watom sample as representative of this island's prehistoric population, and if the recent finding by P. Kirch (1988) is verified elsewhere that Lapita ware shows no developmental sequence in the Mussau Islands, and therefore must have had its origin in South-east Asia as others have suggested, then it would appear that at least some of the Lapita pottery found on Watom represents direct or indirect trade activity with non-Melanesians. This suggestion could not be taken seriously if based only on the Watom and Mussau teeth. However, when all Polynesia is considered, it is quite reasonable, because teeth of all Polynesian groups are significantly more like those of south-east Asians than like Melanesians (Table 2; Turner n.d.b).

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A Lapita-associated Skeleton from Natunuku, Fiji

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ABSTRACT. The fragmentary and generally poorly preserved remains of an approximately 3,000 year old skeleton found in association with Lapita cultural material at Natunuku, Fiji, are described. The skeleton, represented by diaphyseal fragments of the major limb bones, fragments of skull and other parts of the skeleton, isolated teeth and a partially edentulous mandible fragment, is that of an elderly (50 year old) male. The mandible is the best preserved bone in these remains. Stature is estimated to be 172 cm. The limb skeleton suggests that the individual is of moderately robust dimensions. Only minimal expressions of osteoarthritis are observed in these remains but opportunities for observations are limited. The teeth exhibit considerable wear and caries are present. The cause of death cannot be determined. There is no evidence that any of the human remains were burned or charred. Univariate comparisons of morphological details of the skeleton and associated teeth suggest Polynesian similarities such as tall stature, limb robusticity, small tooth crown diameters, and partial rocker jaw. Other aspects of skeletal morphology, limb proportions and the shapes of the leg bones, however, suggest Melanesian affinities. Multivariate analyses of mandibular measurements further suggest Melanesian affinities while similar analyses of a limited number of non-metric traits suggest Polynesian relationships. Until much larger and more representative samples of Lapita-associated skeletons become available, the biological origins of Polynesians, using the human palaeontological record from the Pacific, remains obscure.

PIETRUSEWSKY, M., 1989. A Lapita-associated skeleton from Natunuku, Fiji. Records of the Australian Museum 41(3): 297–325.

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In 1967, Elizabeth Shaw (1967, 1975) excavated a single human skeleton at Natunuku VL1/1, a coastal site located between the villages of Ba and Tavua on the northwest coast of Viti Levu of the Fiji Islands (Fig. 1). Cultural material in the form of potsherds and shells are scattered throughout the site's six levels. The upper four contain material of several origins while the bottom two layers, Levels 5 and 6, have material restricted to the Lapita cultural complex (Green, 1979:33). The skeleton lay undisturbed in a crouched position in a shallow grave in Layer 5, its skull facing north. The earliest levels of the site and the skeletal remains have been dated to 1,590 ± 100 B.C. or 3,240 ± 100 years B.P. (Shaw, 1967 and personal communication, 1984). Green (personal communication, 1989) however, believes that the Natunuku burial, while early in the Fijian Lapita sequence, is probably not as early as the 1,500 B.C. date often assigned to it. Spriggs (personal communication, 1988) has further suggested, based on pottery style, that the Natunuku site is more likely to date to 1,000 B.C. rather than 1,500 B.C. Despite these reservations, the Natunuku skeleton is the earliest Lapita-associated skeleton thus far described. A complete archaeological report on the

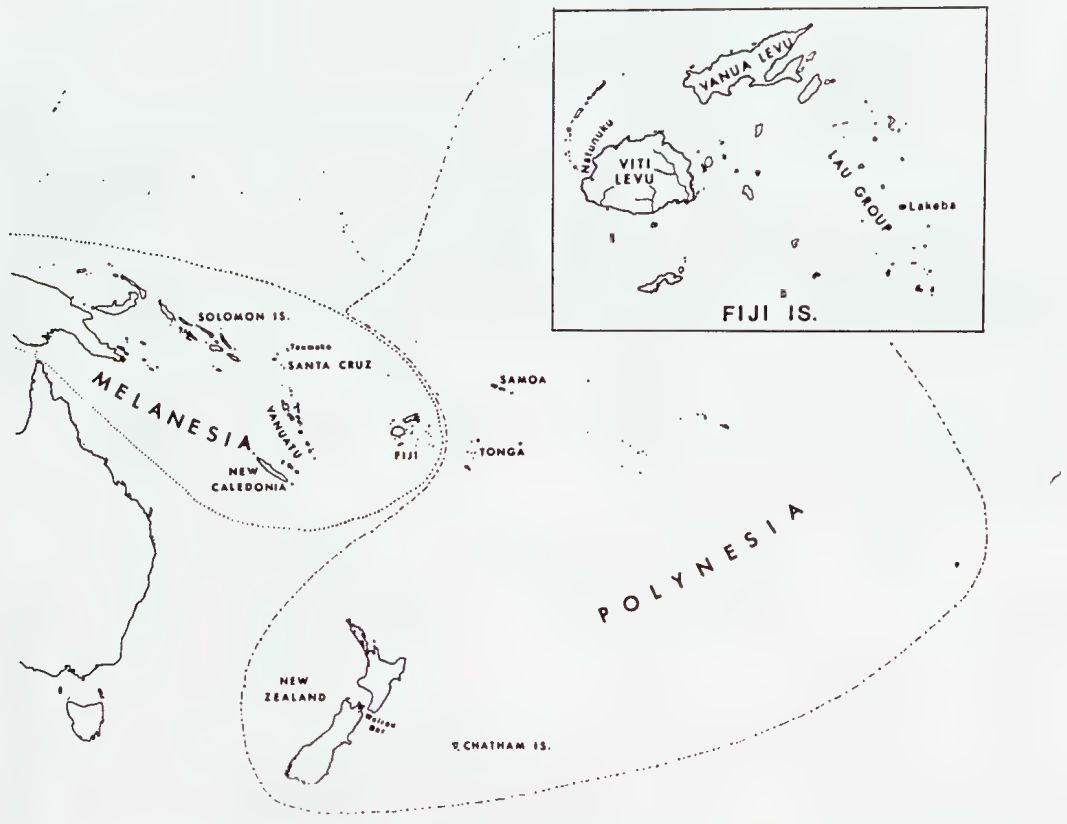

Fig.1. Map showing the location of the Natunuku site and several of the comparative samples.

Natunuku site has not been published.

The Natunuku skeleton was sent to the University of Hawaii in 1970 where it was described in an unpublished B.A. Honours thesis (Filler, 1971). Given the incomplete and preliminary nature of this study and the scarcity of Lapita skeletal remains in general, a re-investigation and re-analysis of the Natunuku skeletal remains was initiated in the early part of 1984 at the University of Hawaii. Since then, only the mandible fragment has been described (Pietrusewsky, 1985a, 1985b). The purpose of the present study is to provide a detailed description of the entire Natunuku skeleton, including an assessment of its age, sex and stature and a notation of the metric and non-metric features of the skull, teeth and infracranial skeleton. Observations of pathology and the results of univariate and multivariate comparisons of the Natunuku skeleton with other skeletal remains from the Pacific are further described.

Appendix A includes all tables referred to in the text.

Material

The human skeletal and dental remains from Natunuku are fragmentary and incomplete. The major bones and teeth of the Natunuku skeleton are shown in Fig. 2.

Except for a few hand phalanges and carpal bones, none of the bones are completely preserved. Judging from the weathered and brittle appearance of these remains, little of the bone's organic content has been preserved. Much of the cancellous bone is either eroded or missing.

During the study of the human remains, fragments of pottery, fish vertebrae, turtle and mammal bones were

Fig.2. An overview of the Natunuku skeleton showing the major bones and teeth present.

identified. Some of the turtle and animal bones have been heated or burned. None of the human bone fragments have been burned as originally reported by Filler (1971). While some of the latter are dark in color, this condition seems to have been caused by post-depositional staining rather than charring.

A preservative which had been applied at the time of excavation retarded further disintegration of this fragile material. However, the preservative, dirt and other foreign particles adhering to most of these remains was not removed prior to Filler's initial reconstruction. In the present re-study, therefore, it was first necessary to remove the preservative and other impurities by immersing the remains, except the mandible fragment, in acetone for 24 hours. While effective in removing the preservative, this treatment further dissolved the adhesive originally used to mend the broken bones, thereby necessitating that these remains be reconstructed a second time. A two-part epoxy binding agent was used in this final reconstruction. Following this procedure, the majority of the diaphyseal shafts of the major limb bones and other parts of the skeleton were reconstructed.

Cranium

Except for two fragments of the occipital bone, a portion of the left zygomatic bone and a part of the frontal bone, most of the cranium is missing. The remaining cranial fragments are too small to permit further identification.

The occipital fragment, measuring approximately 71 mm by 53 mm, preserves a prominently developed inion process externally. Further identified are a portion of the external occipital crest and a small portion of the superior nuchal line. Internally, a portion of the groove for the superior sagittal sinus, the internal occipital crest and a portion of the groove for the transverse process are visible. The right groove is continuous with the groove of the superior sagittal sinus. The fragment is thick, measuring approximately 21 mm at the inion and 10 mm just superior to the external occipital protuberance.

The second largest cranial fragment, a nearly complete left zygomatic bone, preserves the frontal process including the articulation with the frontal bone, the entire orbital border and most of the maxillary border. The temporal process of this bone is only partially complete. A single zygomatico-facial foramen is visible externally. A zygomatico-orbitial foramen is further visible in the orbital surface of this bone. Both the marginal tubercle (located on the lateral surface of the frontal process) and the malar tuberosity (a slightly raised area for the origin of the zygomaticus minor muscle) are moderately developed. The two cranial fragments are shown in Fig. 3.

The third identifiable cranial bone fragment, measuring 35 mm by 27 mm, is from the frontal bone. The fragment preserves the zygomatic process, a portion of the orbital rim and adjoining regions of the squama from the left side of the frontal bone. The internal surface of this fragment is weathered revealing the inner diploic structure.

The remaining small fragments of skull are too fragmentary to permit further identification. Large areas of the vault region and especially the face are missing.

Mandible

The most complete bone of the skull is a reconstructed

Fig.3. Two cranial fragments from the Natunuku skeleton. The thick occipital bone fragment (on left) preserves a well-developed inion process. The fragment on the right is a nearly complete left zygomatic bone.

mandible fragment (see Figs 4-7) which preserves in its entirety the right body and a portion of the adjoining left mandibular body. The latter extends as far as the alveolus of the C/P3 region. The right ramus is missing the coronoid process and the articular head (condyle) of the mandible. The angle of the mandible forms a blunted projection which rests squarely on a level surface posteriorly. Anteriorly, the chin is raised warranting the designation partial 'rocker jaw'. The site for the attachment of the masseter muscle on the external surface of the left ramus is well developed. Externally, a well developed mental protuberance is preserved. Internally, the mental spine (genial tubercle) appears undamaged and single. Given its relatively complete nature, the perservative which was applied at the time of excavation was not removed prior to the present study.

The mandibular fragment is virtually edentulous, only the alveoli for the left canine and right lateral incisor indicate post-mortem tooth loss. The remaining alveoli exhibit complete or fairly advanced states of resorption.

Teeth

Five isolated teeth (Fig. 8) found in association with these

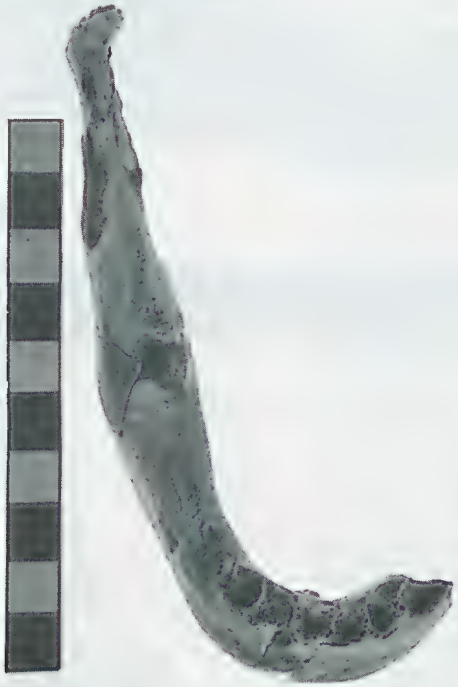

Fig.4. Superior view of the Natunuku mandible fragment.

Fig.5. Lateral (right) view of the Natunuku mandible. The mandible is classified as a partial 'rocker jaw'.

Fig.6. Internal lateral view of the Natunuku mandible fragment.

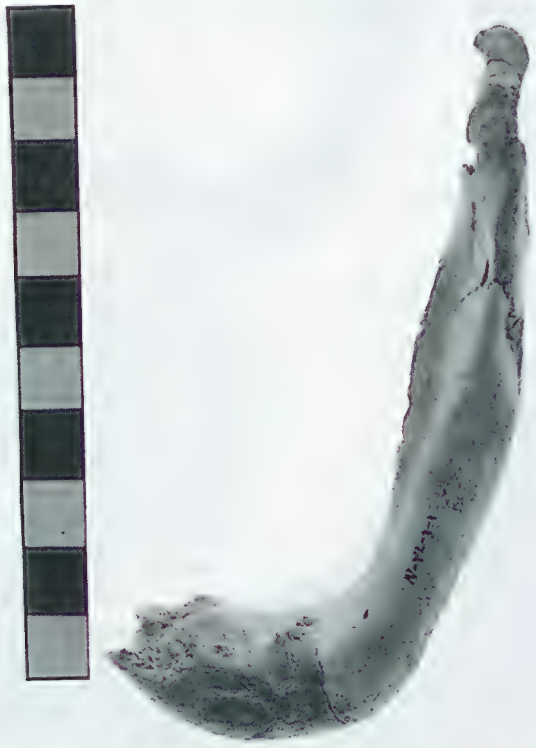

Fig.7. Inferior view of the Natunuku mandible fragment.

remains include a second (right?) molar from the upper dentition and both lateral incisors and the canines from the lower dentition. None of the lower teeth, however, convincingly fit any of the alveolar sockets preserved in the mandible fragment.

Infracranial Skeleton

The infracranial skeleton is represented by reconstructed shaft fragments of the right arm, left forearm, portions of both hands, lower limb bones and a few bones

Fig.8. Isolated teeth found in association with the Natunuku skeleton.

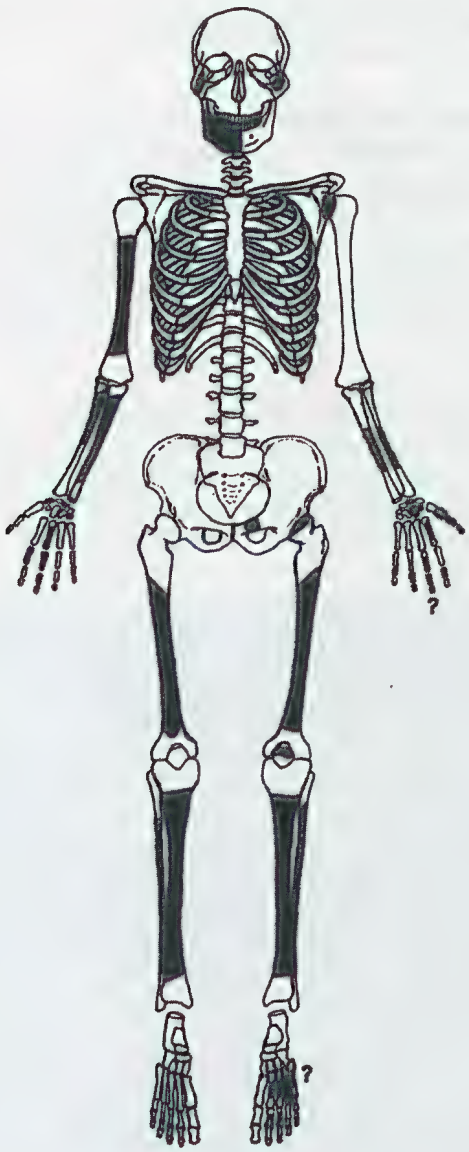

Fig.9. Skull and infracranial representation of the Natunuku skeleton. The darkened areas indicate the parts present.

from the left foot. The bones of the shoulder, thoracic and pelvic regions, except for fragments, are mostly missing. The articular ends of the major limb bones are represented by only a few fragments, none of which can be joined to the diaphyseal shaft fragments of these bones. Hand phalanges and carpal bones are the most complete bones represented in the infracranial skeleton. Skull and infracranial representation of the Natunuku skeleton is shown in Fig. 9. An inventory of the identifable skeletal fragments and teeth is given in Appendix A.

Methods

Age and sex determination follow criteria described in Anderson (1969), Brothwell (1981), and El-Najjar & McWilliams (1978).

Measurements recorded on the mandible and infracranial bones were made using an osteometric board, mandibulometer and sliding calipers. The measurements, indices and angles recorded on the mandible are given in Table 1. The measurements and indices recorded in the infracranial skeleton are explained in Table 2. Helios dial sliding calipers (pointed tips) were used to record the mesial-distal and bucco-lingual crown diameters of the teeth as defined by Moorrees (1957:80). Non-metric observations recorded on the mandible and teeth follow the author's previous work (Pietrusewsky, 1969a, 1969b). Estimation of the maximum lengths of limb bones follow methods explained in Steele (1970). Stature was estimated using formulae based on New Zealand Maori material described in Houghton *et al.* (1975). Where permitted, pathological involvement of bones and teeth were noted. Again, where observations were possible, osteoarthritis of the major articular surfaces of the infracranial skeleton was systematically recorded on an 0, +, ++, +++ basis indicating none, slight, medium and considerable amounts of osteoarthritic lipping, respectively. These categories of osteoarthritic lipping correspond most closely to those described by Brothwell (1981:146-151).

The Natunuku Skeleton

Age estimation. Given the relative incompleteness of these remains, including the absence of the symphysis pubis and the ends of the limb bones, age determination is based primarily on dental observations and the general size of the limb bones. The shafts of limb bones are of robust dimensions suggesting the individual is adult. Hand and foot bones further indicate adulthood but the absence of osteoarthritis in the latter suggests that the age may not be advanced. Four of the five isolated teeth, two mandibular lateral incisors and the two canines associated with the skeletal remains reveal advanced states of dental attrition in which the dentin is exposed suggesting this individual lived to old age (50+ years). The advanced states of alveolar resorption observed in the mandible fragment support this age determination.

Sex determination. Determination of sex was based on the size and robusticity of the infracranial skeleton. Virtually none of the pelvis is present, but the limb bones exhibit strong muscle markings. The existence of strong pilastering of the femur and a strongly developed deltoid tuberosity observed in the right humerus fragment suggest the individual is male. Estimated femur length approximates male Maori femora (Schofield, 1959). A prominently developed inion on the occipital bone further indicates these are the remains of a male.

Cranium. Only two measurements could be recorded in the cranial remains from Natunuku, both on the left zygomatic bone: Inferior Malar Length = 29 mm and Cheek Height = 26 mm. The latter is an estimate given the incompleteness of this bone.

Mandible. The measurements and mandibular indices recorded on the Natunuku mandible are presented in Table 3. Several of the measurements are estimates based on a reconstruction (traced on graph paper) of the missing portions of the mandible using the right side as a template. Using this reconstruction, the mandibular length, maximum bicondylar width and gonial breadth were estimated. The ramus height and mandibular notch breadth (measured on the left side) are the best approximations possible based on the portions of superior ramus present.

Later in this report, the results of multivariate comparisons of the Natunuku mandible with a number of Pacific mandible samples are presented. Here, univariate comparisons of measurements and non-metric observations recorded on the Natunuku and several Pacific samples are summarised. Comparative data for three indices are presented in Table 4.

Mandibular index. As measured by this index, the lower jaw is narrow or dolichognathic. A majority of Polynesian mandibles have broader dimensions. The values recorded for the Gilbert-Marshall Islands, Fiji and Gulf Province (Papua New Guinea) samples are most like the index value recorded for the Natunuku mandible.

Gonio-condylar index. The relatively high value obtained for this index indicates that the ascending rami of the Natunuku mandible are not very divergent. Again, of the values presented in Table 4, the Gilbert-Marshall Islands sample is closest to the value recorded for Natunuku. The ascending rami of Polynesian mandibles are generally more divergent.

Ramus index. This index, which is an approximation of the relative breadth of the ramus to its height, obtains a medium value indicating that the Natunuku ramus is neither especially elongated nor low. Compared with the other Pacific groups, this value is closest to those recorded for New Britain and Vanuatu although the observed variation in this index is not extreme.

The angle formed by the ramus relative to the horizontal plane is acute in the Natunuku mandible. The angle measured at the symphysis is equally low indicating a non-prognathic lower jaw.

Non-metric features. Non-metric features of the mandible include a single mental foramen on both sides. No bridging of the mylo-hyoid line is observed on the right side. The mandibular foramen on the right side is single. The lower border of the mandible is convex causing the mandible to 'rock' when it is deflected anteriorly from a resting position on a level surface. The mandible does not 'rock' when deflected posteriorly. A strong mandible angle and slight gonial eversion further warrant the designation 'partial rocker jaw'. A comparison of the non-metric traits recorded in the Natunuku mandible with three other Lapita-associated mandibles is presented in Table 5. The latter show a remarkable similarity in their non-metric variation.

Bridging of the mylo-hyoid line, multiple mandibular and mental foramina and mandibular tori are uniformly absent in all mandibles. All Lapita-associated mandibles are classified as partial 'rocker jaws'. The chin usually forms a bilateral prominence anteriorly.

A multivariate comparison of the non-metric observations recorded on the Natunuku mandible with other Pacific mandibles is presented later.

Dental status of mandible. The mandible fragment exhibits considerable alveolar resorption, especially in the posterior region. No teeth were found in the mandible at the time of this study. The socket for the right third molar, lost pre-mortem, exhibits a partially healed abscess. The remaining molars, premolars and the canine tooth from the same side were lost well in advance of the individual's death; their alveolar sockets have been completely resorbed. The socket for the right lateral incisor is still evident suggesting post-mortem loss of this tooth. The two central incisors and the left lateral incisor were lost not very long before the death of the individual and their sockets reveal the first stages of alveolar resorption. The socket for the left third molar exhibits less resorption. The socket for the left canine suggests that this tooth was lost post-mortem. The remaining portion of the mandible preserves a completely resorbed socket for the right first premolar (P3).

Except for the aforementioned alveolar erosion observed in the third molar socket, there is little evidence of abscessing in the mandible fragment. However, given the resorption of the alveolar sockets, opportunities for observing periodontal disease in the mandible fragment were few.

Isolated teeth. The root and particularly the cervical regions of the five isolated teeth found in association with the skeletal remains of this individual exhibit a reddish-brown stain. Small amounts of calculus (tartar) formation at or below the cemento-enamel junction are further observed in these teeth.

As mentioned earlier, the state of alveolar resorption in the mandible suggests that the left canine and right lateral incisor were probably lost post-mortem. None of the isolated teeth, however, were found to fit convincingly any of the existing mandibular alveolar sockets. It is therefore not known for certain if any of the isolated teeth belong to this skeleton. Given that the anterior teeth are more greatly

worn than the single molar tooth, two individuals may be represented.

Individual observations of the teeth follow:

7 The enamel portion of this tooth is slightly worn. Interproximal caries are observed on the mesial surface of the crown just superior to the crown/root junction and at the cervix on the lateral (buccal) side of the tooth. The molar cusp pattern in this tooth is +5.

3 Advanced attrition of this tooth's distal occlusal surface produces an uneven (oblique) wear pattern which exposes the dentin. Such unequal wear has sometimes been observed to occur in advanced stages of dental attrition (Brothwell, 1981:72). No caries are observed in this tooth.

2 The occlusal surface of this tooth is evenly worn well into the dentin. There is a small interproximal cervical caries on the mesial surface.

2 The dental attrition seen in this tooth mirrors that observed in the incisor from the opposite side. Again, small interproximal cervical caries are evident on the mesial surface.

3 As was observed in the other canine, this tooth exhibits uneven wear exposing the dentin. The tooth has no caries.

Measurements recorded on the isolated teeth are presented in the Table 6.

Some comparative data recorded on Asian and Pacific samples are presented in Tables 7 to 9. Crown diameters of the Natunuku teeth are similar to Asian and Polynesian teeth.

Infracranial skeleton. Measurements recorded on the infracranial remains for the Natunuku skeleton are presented in Table 10. Infracranial indices and estimations of stature are presented in Table 11. Some comparative data recorded on a number of Pacific Island samples are given in Table 12.

Humerus. The right humerus fragment extends approximately from the region of the deltoid tuberosity to the supratrochlear region, its closest approximation is Steele's humerus shaft segment-2 (Steele, 1970). The fragment is of robust dimensions, an observation that is supported by the high value obtained for the index of robustness. The diaphysis displays little or no flattening.

The humeral-femoral index is low indicating that arm length is proportionately shorter than leg length. In this instance, the Natunuku skeleton approaches the mean values recorded for Nebira and Tonga.

Radius and ulna. These bones are represented by shaft fragments from both forearms. The bones are too incomplete and fragmentary, however, for maximum lengths to be determined. The shaft diameters of these bones suggest an individual of robust proportions.

Femur. Extensive reconstruction yielded the major shaft fragments of both femora, they approximate Steele's shaft fragment-3. The mid-shaft region of both femora display strong pilastric development, indicating a strongly developed linea aspera. The values of this index exceed all values presented in Table 12 except the one recorded for Fiji. Further, there is no flattening (platymeria) in the subtrochanteric region of the Natunuku femora as is typical of Polynesian thigh bones. The shapes of the Natunuku femora are most like those in the Nebira sample. Natunuku femur robustness is most like that recorded for the Fiji, Nebira and the Marquesas samples. While the femoral shafts appear bowed (see Fig. 10), low values were obtained for the bowing index.

Strong pilastric development and missing extremities are at least partially responsible for the results obtained here.

Tibia. The tibial shafts display little or no flattening (platymeria) at the level of the nutrient foramina. Table 12 indicates that the Natunuku tibiae are the least flattened of all the samples compared and that they are most like the Nebira tibiae. The tibia (lower leg) length expressed as a

Fig.10. Femoral shaft fragments (right and left) from Natunuku.

percentage of the femur (thigh) length (Crural index) is proportionately greater in the Natunuku skeleton than in any of the other Pacific groups compared. This proportion is again closest to those reported for Fiji and Nebira.

Non-metric features. Given the highly fragmentary and incomplete condition of the infracranial skeleton, no observations of the non-metric characteristics are possible.

Stature. Using formulae devised by Houghton *et al.* (1975), living stature is estimated to be approximately 172.4 cm or 5 feet 8 inches. The formulae used are given in Table 11. Compared with other male Pacific groups, the skeleton from Natunuku is closest to the stature estimated for a number of Polynesian groups.

Pathology. Descriptions of dental pathology were presented in the section on dentition. Given the incomplete and fragmentary nature of these remains, systematic recording of pathological involvement in the infracranial skeleton is limited. Almost none of the extremities of the major limb bones are preserved. Evidence of osteoarthritis in the carpal and metacarpal bones, some of the best preserved bones, is minimal or nonexistent. Other abnormalities, such as bowing of the lower limb bones, is discussed in the section dealing with the infracranial skeleton. The cause of death cannot be determined.

Multivariate Comparisons

In this section the results of multivariate comparisons using metric and non-metric traits recorded on mandibles are presented.

Mandibular measurements. The detailed results of two separate multivariate comparisons, which utilise measurements recorded on the Natunuku mandible fragment, a Lapita-associated mandible from Lakeba in the Fiji Islands, and several other prehistoric and near-contemporary mandible samples from Polynesia, Micronesia, and Melanesia are presented in an earlier paper (Pietrusewsky, 1985b). The results of this earlier investigation are briefly reviewed here to allow comparisons with the results obtained through univariate and multivariate comparisons of other aspects of the Natunuku skeleton.

Multivariate procedures [Mahalanobis' Generalised Distance (Mahalanobis, 1936) and stepwise discriminant function analysis (Dixon & Brown, 1979)] applied to seven mandible measurements recorded on seven male samples are discussed first. The means of the seven measurements for these samples and their provenance are presented in Table 13.

The diagram of relationship which results from a cluster analysis of the d-squared results is shown in Fig. 11. The two Lapita-associated mandibles from Natunuku and Lakeba form a loose association. Additionally, very close associations between prehistoric Wairau Bar and near-contemporary New Zealand Maori and between the prehistoric Tongan and Namu samples is indicated in this diagram. Further clarification of these relationships is presented in the next diagram, Fig. 12, which summarises the results of stepwise discriminant function analysis. Natunuku and Lakeba are closest to the Namu and Tongan samples, all of which are well separated from the samples in

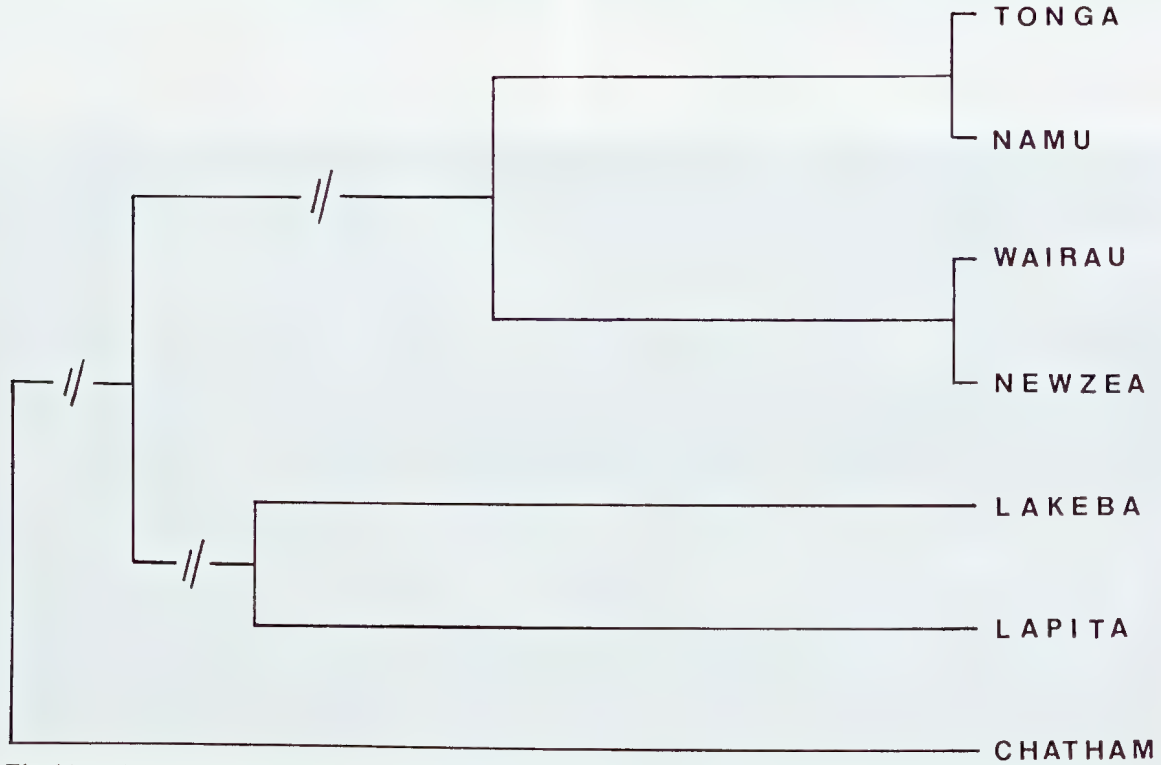

Fig.11. Diagram of relationship of d-squared results for 7 male samples using 7 mandible measurements.

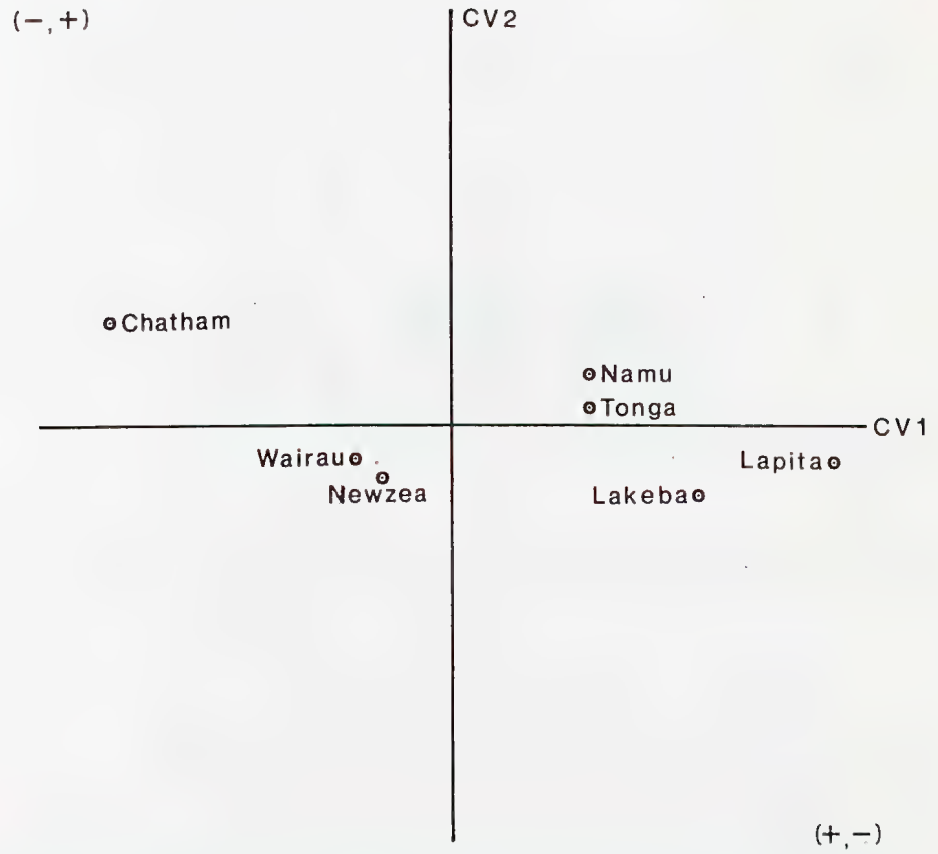

Fig.12. Plot of 7 male means on the first and second canonical variables using 7 mandible measurements (stepwise discriminant function analysis).

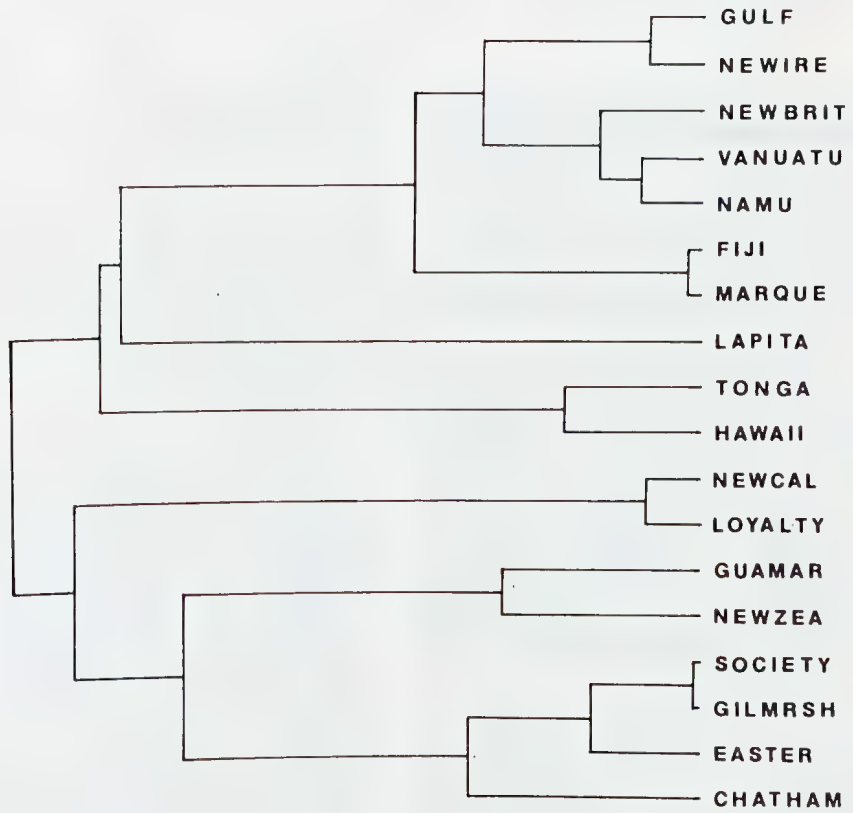

Fig.13. Diagram of relationship of d-squared results for 18 male samples using 5 mandible measurements.

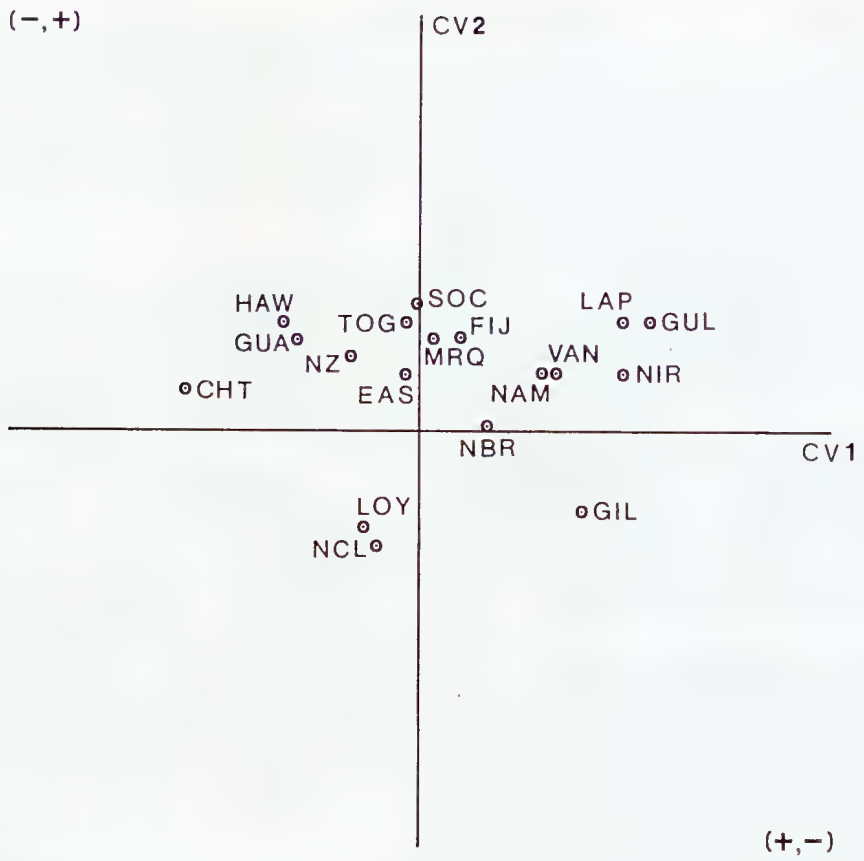

Fig.14. Plot of 18 male means on the first and second canonical variables using 5 mandible measurements (stepwise discriminant function analysis).

western Polynesia.

In the second analysis the same multivariate procedures are applied to five mandibular measurements recorded on eighteen male samples. With the exception of Natunuku, Tonga and Namu, the samples are not well dated, the majority represent near-contemporary specimens found in museums located in Europe, Australia, New Zealand and Hawaii. The sample sizes and means for the five mandible measurements recorded for these groups are presented in Table 14.

A cluster analysis of Mahalanobis' d-squared values is presented in Fig. 13. The main separation in this diagram is between a basically Polynesian-Micronesian constellation and a Melanesian cluster. Natunuku, while somewhat peripheral, associates with the Melanesian subdivision. Multiple discriminant function analysis (Fig. 14) reiterates this separation and underscores Natunuku's proximity to the Melanesian grouping. Two samples from eastern Melanesia, the Loyalty Islands and New Caledonia, form a separate isolate unrelated to any of other samples included in the analysis.

Non-metric traits. In this section, multivariate procedures are applied to three non-metric mandibular traits. The non-metric observations which were recorded on the Lapita-associated mandibles and a number of Pacific and Asian groups are presented in Table 15. With the exceptions given in Table 15, these data are taken from Pietrusewsky (1984). Using a computer program written by Molto (1980), the Mean Measure of Divergence statistic, or MMD, (Green & Suchey, 1976) is applied to non-metric traits as an alternative means for assessing group relationships. Six separate applications, representing various partitions of the larger data set, were made. Using an unweighted pair-group clustering technique, diagrams of relationship based on the MMD results are constructed using a computer program written by Dr Jim Archie of the University of Hawaii. The results of each distance analysis are presented separately.

Seven male samples, three non-metric traits. This analysis, which applies the MMD statistic to three non-metric traits recorded on seven male samples, most nearly approximates the samples used in the multivariate analysis of seven mandible measurements presented earlier. The diagram of relationship of these results (a cluster analysis of the MMD Scores) is shown in Fig. 15.

The two Lapita-associated samples from Natunuku and Lakeba form a separate cluster in this diagram. Namu and Tonga occupy the most peripheral positions. The relatively high incidence of non-rocker jaw in the Namu sample is chiefly responsible for the isolation of this sample. The Wairau Bar sample similarly occupies a marginal position in this diagram.

Eighteen male samples, three non-metric traits. This

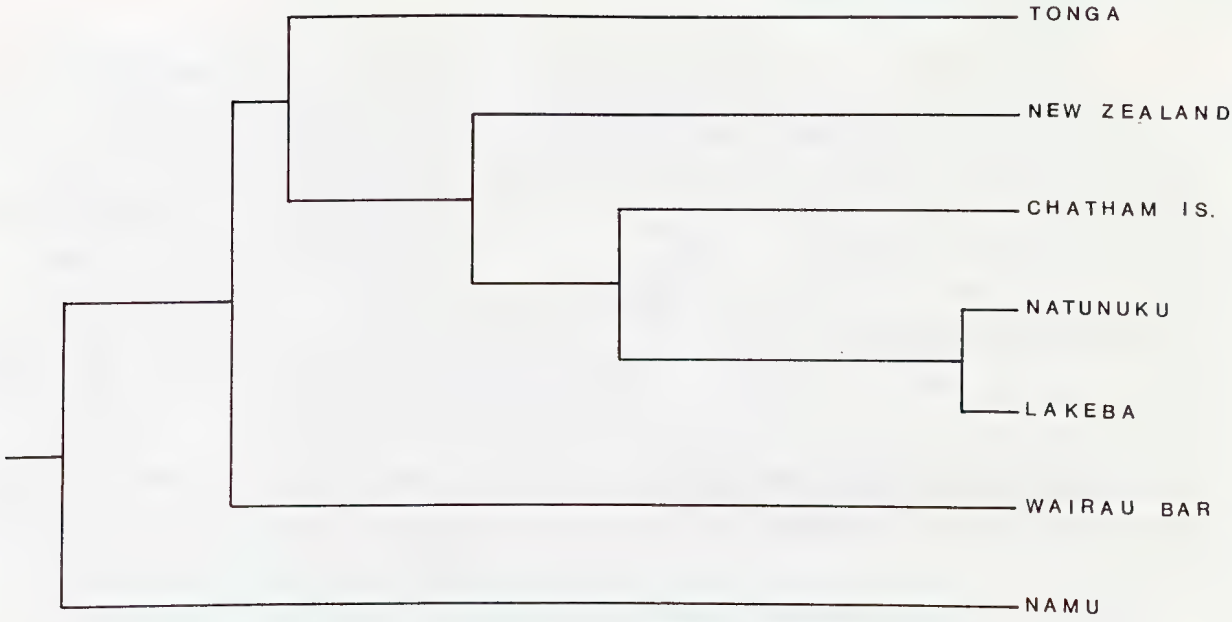

Fig.15. Diagram of relationship of Mean Measure of Divergence (MMD) results for 7 male samples based on 3 mandibular non-metric traits.

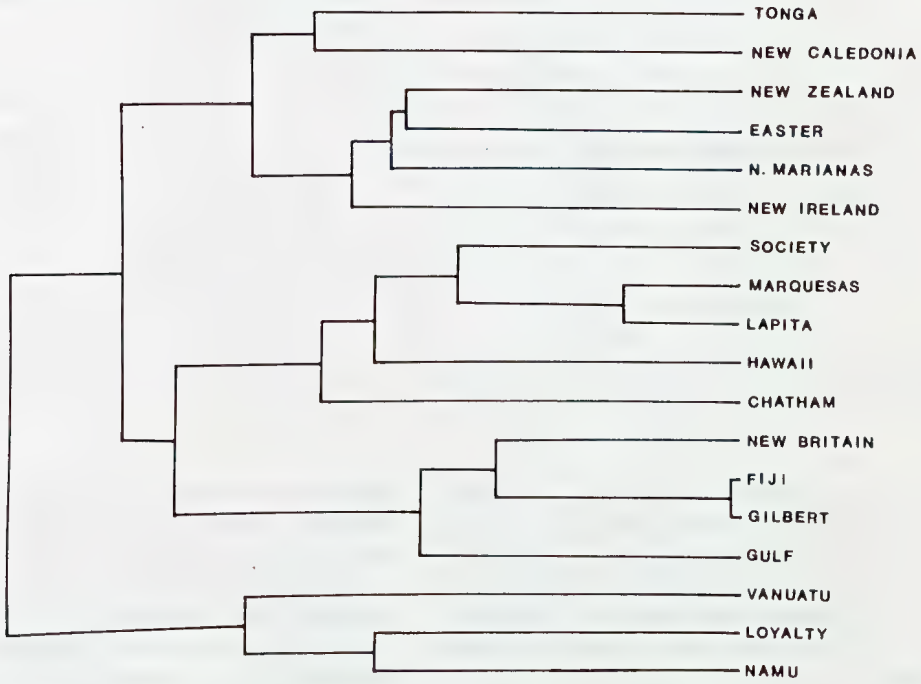

Fig.16. Diagram of relationship of Mean Measure of Divergence (MMD) results for 18 male samples based on 3 mandibular non-metric traits.

comparison most nearly approximates the samples analysed in the larger metric analysis. The diagram of relationship is given in Fig. 16. The Lapita sample falls within a cluster containing samples from eastern Polynesia and is closest to the prehistoric Hane Dune (MUH-1) sample from Uahua, Marquesas. The groups which are next closest to this cluster, containing the Natunuku mandible, are New Britain, Fiji, Gilbert-Marshall and Gulf. No recognisable patterning among the remaining samples is evident. Samples from eastern Melanesia (Vanuatu, Loyalty, Namu and New Caledonia) occupy isolated positions in the diagram. Inspecting the original MMD values (not shown) identifies the Gilbert-Marshall sample as the one closest to the Lapita sample.

Eight male samples, three non-metric traits. The results of applying the MMD statistic to non-metric traits recorded on eight male samples is given in Fig. 17.

The Lapita and Marquesas (Hane Dune) sample form a close association which, in turn, attracts samples from eastern and marginal Polynesia. Tonga and Fiji represent a western division.

Ten male samples, three non-metric traits. In this analysis, Lapita mandibles are compared with Melanesian samples.

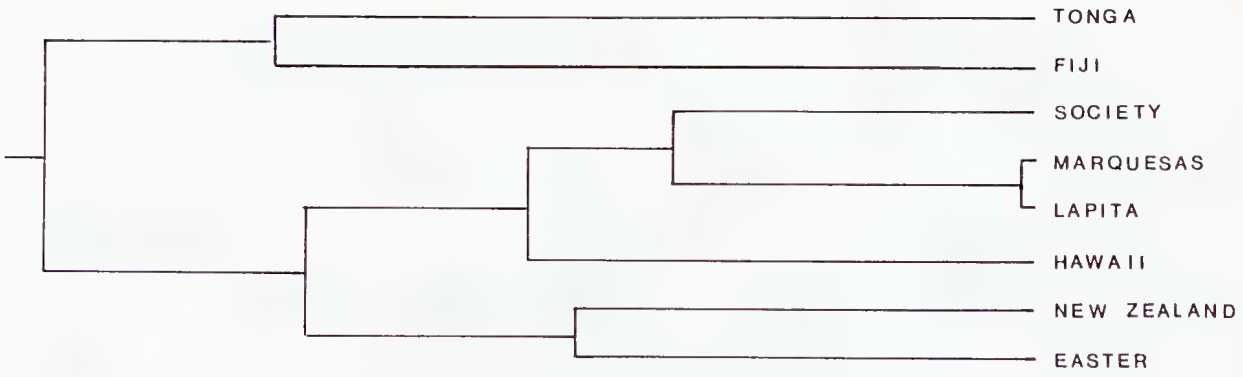

Fig.17. Diagram of relationship of Mean Measure of Divergence (MMD) results for 8 Polynesian male samples based on 3 mandibular non-metric traits.

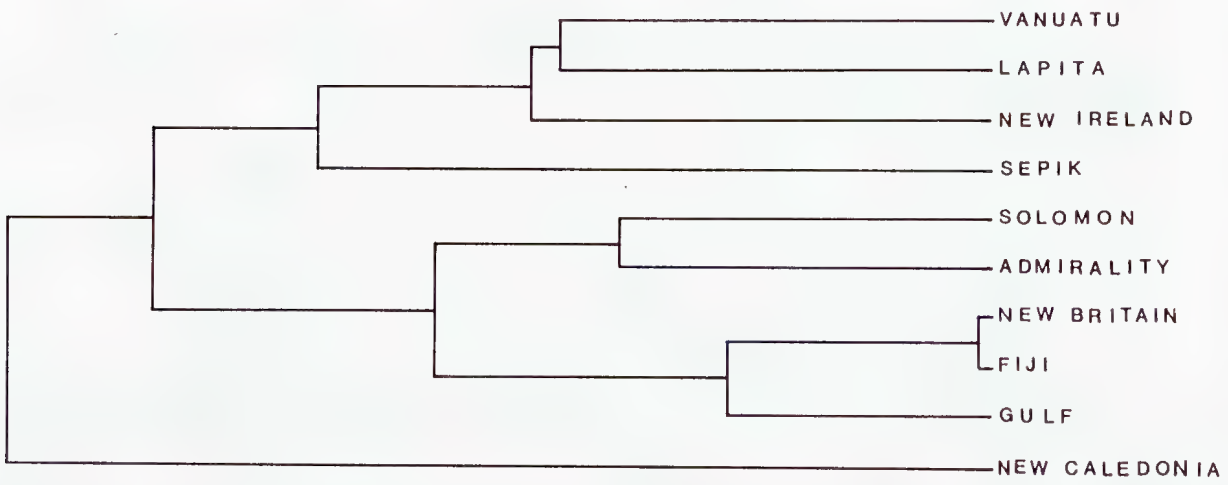

Fig.18. Diagram of relationship of Mean Measure of Divergence (MMD) results for 10 male Melanesian samples based on 3 mandibular non-metric traits.

The diagram of relationship is presented in Fig. 18. The Lapita sample falls within a cluster which contains, with the exception of Vanuatu, samples from western Melanesia. Inspection of the MMD results (not shown) further reveals that the samples nearest to the Lapita sample are Solomon, Gulf, Sepik, New Ireland and Admiralty. The samples from eastern Melanesia are the most removed from the Lapita sample.

Ten male samples, three non-metric traits. The results of applying the Mean Measure of Divergence statistic to three non-metric traits recorded on the Lapita mandibles and nine corresponding samples from South-east Asia and East Asia are presented in Fig. 19. Lapita mandibles are found to cluster with samples which are largely of island South-east Asian origin. The groups closest to the Lapita sample are the Philippines, Borneo and Sulu.

Twenty six male samples, three non-metric traits. Finally, including all the samples used in the previous three analyses, the MMD statistic is applied to 26 male samples. The diagram of relationship based on the MMD scores is presented in Fig. 20. In this representation, the Lapita and Hane Dune (Marquesas) samples form a close connection. Other samples which demonstrate an affinity to the Lapita sample, as interpreted by this diagram and inspection of the MMD values (not shown) include the Society Islands, Hawaii, Sepik and Gulf. With the exception of New Caledonia, New Britain and Fiji, the remaining samples form three groupings which are equidistant from the cluster containing the Lapita-associated mandibles.

Discussion and Conclusions

Despite the incompleteness and variable preservation of the 3,000-3,500 year old Lapita-associated skeleton from Natunuku and the limitations of using a single specimen, comparing this material with other prehistoric and near-contemporary inhabitants of the Pacific allows some tentative conclusions regarding biological relationship and Polynesian ancestry.

The relatively tall (172 cm or 5 feet 8 inches) stature and the robustness of the Natunuku appendicular skeleton is consistent with a Polynesian physical pattern (Houghton,

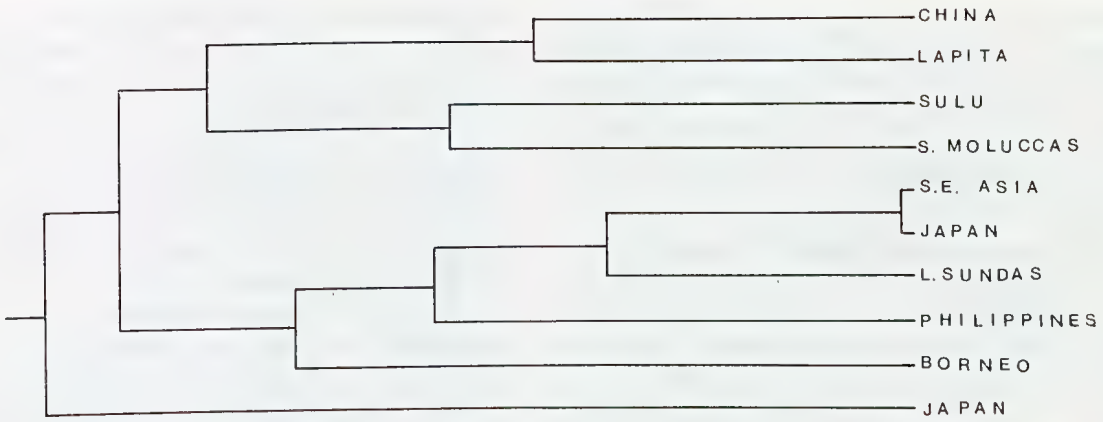

Fig.19. Diagram of relationship of Mean Measure of Divergence (MMD) results for 10 male samples based on 3 mandibular non-metric traits.

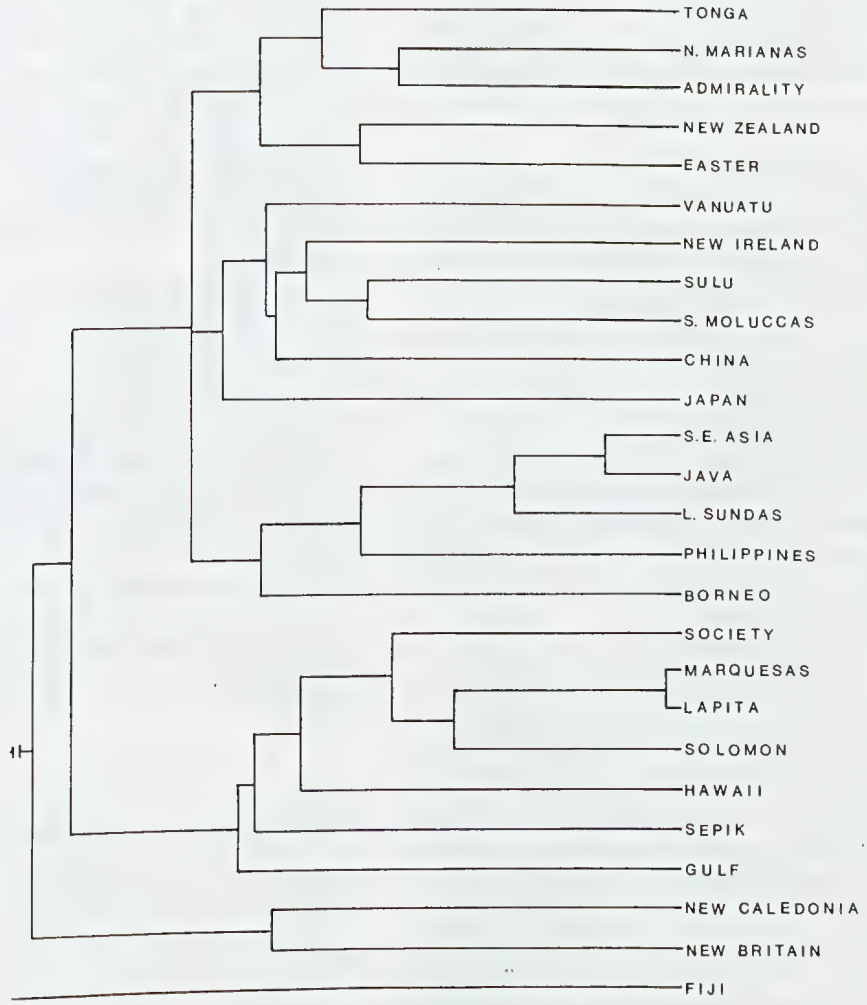

Fig.20. Diagram of relationship of Mean Measure of Divergence (MMD) results for 26 male samples based on 3 mandibular non-metric traits.

1980: 67-78). Other aspects of the Polynesian physical form such as relatively short legs and bowing of the limb bones are not observed in the Natunuku skeleton. In fact, the size, shape and relative proportions of the Natunuku lower limb bones are closest to Melanesian samples such as Fiji and Nebira. Of the Polynesian groups compared in Table 12, the Marquesas is most like Natunuku. Much of our knowledge of the Polynesian limb skeleton is based on New Zealand Maori material (Schofield, 1959; Houghton, 1980) which, as the comparative data used in the present

study indicate, may not be entirely typical of Polynesians. This seems to be particularly true for the shape (platymeric index) of the femur's shaft which is considerably flattened in the New Zealand Polynesian femur but is of more rounded proportions in other parts of Polynesia. This is also true of the Natunuku femur shaft which is most like Tongan and New Guinea femora.

Further, the strong pilaster development observed in the Natunuku femora is not consistent with the Polynesian pattern. In this respect, Natunuku is again closest to Fiji. Femur robustness in the Natunuku skeleton is most like that recorded for Fiji, Nebira and the Marquesas. While the femoral shafts of the Natunuku skeleton appear to be bowed, this is not reflected in the values obtained for the bowing index. The shapes of the tibial shafts in the Natunuku skeleton again are most like the values obtained for Nebira, a sample from coastal Papua New Guinea.

The crown diameters of the five isolated teeth found in association with the Natunuku skeleton are most like those recorded for Polynesian and East Asian groups (Brace & Hinton, 1981). Unfortunately, the marked attrition found in the teeth prevents comment on the non-metric features of the dentition.

Finally, there is the mandibular fragment, one of the most complete bones of the Natunuku skeleton. Univariate comparisons of metric and non-metric features of this bone indicate that the Natunuku mandible is most like the Lapita-associated mandibles from Tonga and Lakeba and to Polynesians, in general. There is a uniform absence of multiple mental foramina and bridging of the mylo-hyoid line in all Lapita-associated mandibles examined. The presence of a partial rocker jaw condition is further representative of these mandibles.

Unlike Polynesian mandibles, however, the Natunuku mandible is of small dimensions and univariate comparisons place it with mandibles from the Marshall-Gilbert and Fiji Islands. The edentulous condition of the specimen undoubtedly accounts for some of its smallness, particularly the height of the mandible body.

The most extensive comparisons, which involve the application of multivariate procedures to metric and non-metric traits recorded in mandibles, again suggest that there is a basic uniformity among the Lapita mandibles from Fiji and western Polynesia. However, slightly different patterns of relationship are found when multivariate procedures are applied to metric and non-metric variation recorded in the Lapita-associated mandibles and a larger number of Pacific and circum-Pacific samples. Metrically, Lapita mandibles are most like those from Melanesia, especially Gulf, New Ireland, Vanuatu and Fiji, while the results based on multivariate analyses of a limited number of non-metric traits suggest Polynesian affinities. Both sets of results, however, do allow for some intermediate placement of the Lapita mandibles with respect to both Melanesia and Polynesia. For example, the Marquesas, Tonga and Hawaii samples are members of a larger cluster which further contains the Natunuku mandible in Fig. 13 (the results based on measurements). Likewise, despite the overall affinity with Polynesian groups in the non-metric analysis, these same results further indicate that Gulf and New Ireland are about as close to Lapita mandibles as New Zealand and Easter Island.

Earlier conclusions (Pietrusewsky, 1985b), which were based solely on the application of multivariate procedures to mandibular measurements, may warrant reconsideration. In this earlier study, because of the great attraction of the Natunuku mandible to Melanesian samples and its dissimilarity with Polynesian mandible samples, it was argued that it was impossible to derive Polynesians from Melanesians. This view runs counter to the evidence from archaeology which now suggests that the Lapita culture developed indigenously in the Bismarck Archipelago region in north-western Melanesia (e.g. Spriggs, 1984). It is, however, supported by a wealth of evidence from previous studies in physical anthropology (e.g. Howells, 1970, 1973, 1979; Pietrusewsky, 1983, 1984; Serjeantson, 1984; Katich & Turner, 1974; Turner, 1982; Brace & Hinton, 1981) and, more recently, by papers presented at the Micronesian Archaeological Conference held on Guam in 1987 (Brace, n.d.; Howells, n.d.; Turner, n.d.; Pietrusewsky, n.d.). These latter include studies of anthropometric data, cranial variation, genetic data and dentitions of Pacific peoples, all of which identify Polynesians as being genetically uniform and unrelated to Melanesians.

The present study, which examines a single skeleton, cannot completely rule out the possiblity that Polynesians could have developed out of Melanesians. Multivariate analyses of mandible measurements and features of the lower limb skeleton argue against such a derivation, while other aspects of the Natunuku skeleton's morphology, notably stature, skeletal robustness, tooth size, and the non-metric features of the mandible suggest a Polynesian likeness. The Natunuku skeleton, the oldest and most complete skeleton associated with the Lapita culture thus far discovered, cannot, by itself, settle the question of Polynesian origins. As this study clearly demonstrates, additional Lapita-associated skeletons from the Pacific are required for understanding of Polynesian biological origins.

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Appendix A

Table 1. List of mandibular measurements, indices & angles.

	Abbrev	Measurement	Reference
1.	MANDLNTH	Mandibular length (superior)	Olivier, 1969
2.	INFMANDL	Inferior length	Martin -68
3.	ALVEOLGT	Alveolar length	Trinkaus, 1978-BCAB
4.	BICONDWD	Bicondylar width (max. breadth)	Martin -65
5.	MIDCONDW	Bicondylar articular breadth	Trinkaus, 1978-BCAB
6.	CORONBTH	Bicoronoid breadth	Martin -65(1)
7.	BIGONIAL	Bigonial breadth	Martin -66
8.	BICANBTH	Bicanine external breadth	Trinkaus, 1978-CEB
9.	FRMOLBTH	Bimolar-1 external breadth	Trinkaus, 1978-M1EB
10.	THMOLBTH	Bimolar-3 external breadth	Trinkaus, 1978-M3EB
11.	SYMPHYHT	Symphyseal height	Martin -69
12.	MENFORHT	Mental foramen height	Martin -69(1)
13.	CANINEHT	Canine height: at C/P3	Trinkaus, 1978-CHC
14.	MOLARHGT	Molar height: at M1/M2	Martin -69(2)
15.	SYMPHYBT	Symphyseal breadth	Trinkaus, 1978-CBS
16.	MENFORBH	Mental foramen breadth	Martin -69(3)
17.	CANINEBH	Canine breadth: at C/P3	Trinkaus, 1978-CBC
18.	MOLARBTH	Molar breadth: at M1/M2	Trinkaus, 1978-CBM
19.	RAMUSHGT	Ramus height	Martin -70
20.	RAMUSBTH	Ramus breadth	Martin -71
21.	MANDNOTB	Mandibular notch breadth	Martin -71(1)
22.	CONDYLGT	Condyle length	Brown, 1982-I100
23.	CONDYBTH	Condyle breadth	Brown, 1982-I101
24.	PMMOLARL	P3-M1 length	Brown, 1982-I103
25.	MOLARLGT	M1-M2 length	Brown, 1982-I104

Index or Angle	Source
Mandibular = total length/bicondylar breadth	Olivier, 1969
Gonio-condylar = bigonial breadth/bicondylar breadth	Olivier, 1969
Ramus = ramus breadth/ramus height	Olivier, 1969
Mandibular angle = gonial angle formed by ramus on horizontal plane	Olivier, 1969
Symphyseal angle = most acute angle between the horizontal plane and chin	Olivier, 1969
Index of robustness = maximum thickness/body height at mental foramen	Olivier, 1969

Table 2. List of infracranial measurements and indices.

	Source
Humerus	
Maximum length	M-1*
Maximum diameter at mid-shaft	M-5
Minimum diameter at mid-shaft	M-6
Maximum diameter at deltoid	M-6a
Shaft circumference	M-7a
Radius	
Proximal sagittal diameter	M-5
Proximal transverse diameter	M-4
Shaft circumference	M-5(5)
Ulna	
Dorsoventral diameter	M-11
Transverse diameter	M-12
Femur	
Maximum length	M-1
Anterior-posterior diameter-subtroch.	M-10
Medio-lateral diameter-subtroch.	M-9

Table 2 (cont'd).

	Source
Femur	
Anterior-posterior diameter-midshaft	M-6
Medio-lateral diameter-midshaft	M-7
Bowing	Schofield (1959:95)
Tibia	
Maximum length	M-1a
Anterior-posterior diameter-nut. for.	M-8a
Medio-lateral diameter-nut. for.	M-9a
Anterior-posterior-midshaft	M-8
Medio-lateral diameter-midshaft	M-9
Patella	
Thickness	M-3
Lunate	
Maximum length	M-1
Maximum breadth	M-2
Maximum height	M-3
Trapezium	
Maximum thickness	T-1**
MC-1 articular breadth	M-4
MC-1 articular height	M-5
Trapezoid	
Maximum length	M-1
Maximum breadth	M-2
Maximum height	M-3
Hamate	
Maximum height	M-3
Articular length	M-1
MC-4/5 articular breadth	M-8
Capitate	
Articular length	M-4
Maximum breadth	M-2
Maximum height	M-3
Hand Phalanges	
Length	M-1
Height	M-2
Breadth	M-3

Humeral index of robustness = circum./max length x 100	Olivier, 1969:227
Humeral diaphyseal index = min/max diam. x 100	Olivier, 1969:227
Crural index = tibia/femur x 100	Olivier, 1969:269
Humeral-femoral = humerus/femur x 100	Olivier, 1969:262
Femoral index of robustness = trans + A-P midshaft diam./length x 100	Olivier, 1969:262
Platymeric index = A-P/trans. diam. x 100 (subtroch.)	Olivier, 1969:263
Pilastric index = A-P/trans. diam. x 100 (midshaft)	Olivier, 1969:263
Tibial thickness index = trans./A-P diam. (midshaft)	Olivier, 1969:272
Platycnemic index = trans./A-P diam. (nut. for.)	Olivier, 1969:271

* Martin & Saller (1957) number
** Trinkaus (1978)

Table 3. Measurements and indices recorded in Lapita mandible fragments (in mm.).

Measurement	Natunuku	Tonga	Lakeba #1	Lakeba #2
MANDLNTH	108*	–	–	–
INFMANDL	68	–	64	–
ALVEOLGT	71	54.8*	–	–
BICONDWD	114*	124	–	–
MIDCONDW	–	–	–	–
CORONBTH	–	100*	–	–
BIGONIAL	100*	109*	–	–
BICANBTH	37	31.8	–	–
FRMOLBTH	–	54.9	–	–
THMOLBTH	–	68*	–	–
SYMPHYHT	26	27.5*	28	30
MENFORHT	19	24.6**	28	32
CANINEHT	22	29.1	29	32
MOLARHGT	–	27.2	28	29
SYMPHYBT	14	–	14	13
MENFORBH	11	–	11	11
CANINEBH	12	–	10	9
MOLARBTH	13	–	13	13
RAMUSHGT	60*	–	–	–
RAMUSBTH	33	41	31	–
MANDNOTB	37*	–	–	–
CONDYLGT	–	–	–	–
CONDYBTH	–	–	–	–
PMMOLARL	–	–	15	14
MOLARLGT	–	–	18	–
Index, Angle				
Mandibular	94.7	–	–	–
Gonio-condylar	87.7	–	–	–
Ramus	55	–	–	–
Mandibular angle	97°	89°	–	–
Symphyseal angle	72°	–	–	–
Robustness	63	–	–	–

* estimated measurements.
** Spennemann (1985:14) reports a value of 15.2 mm for this measurement while the value given here is his premolar height.

Table 4. Mandibular indices for a number of Pacific groups.

Group	Mandibular Index	Gonio-Condylar Index	Ramus Index
Natunuku	94.7	87.7	55.0
Tonga	87.3	80.1	56.4
Namu	82.6	80.6	52.3
Wairau Bar	90.6	70.8	56.0
New Zealand	82.0	83.4	53.0
Chatham Is.	83.0	88.5	52.9
Society Is.	89.2	81.3	58.9
Marquesas	91.8	83.8	57.2
Easter Is.	86.1	79.2	63.8
Hawaii	85.7	82.7	54.0
Fiji	94.0	83.9	57.6
Gilbert/Marshall	94.7	87.0	57.5
Guam	88.7	85.1	58.2
Gulf, PNG	93.8	82.4	50.9
New Britain	90.6	83.0	54.8
New Ireland	92.0	81.5	53.0
New Caledonia	–	82.6	60.2
Loyalty	–	85.0	60.6
Vanuatu	–	80.4	54.9
China	–	83.6	55.9
South-east Asia	–	82.9	55.9
Thailand	–	82.7	53.4
Mongolia	–	85.4	55.4
Java	83.0	82.7	54.0
Sulu	–	83.2	54.6
Western Australia	94.5	83.4	53.5

Table 5. A comparison of non-metric traits recorded in Lapita-associated mandibles.

	Natunuku	Lakeba[1]		Tonga[2]
		#1	#2	
Mandibular torus	absent	absent	absent	–
Mylohyoid groove-R	no bridge	no bridge	–	no bridge
Mylohyoid groove-L	–	–	–	–
Mandibular foramen-R	single	single	–	single
Mandibular foramen-L	–	–	–	–
Mental foramen-R	single	single	–	single
Mental foramen-L	–	–	single	single
Rocker jaw	anterior	anterior	anterior	anterior*
Chin form	MBA**	BA***	BA	–

[1]Observations recorded by the author on two Lapita-associated mandibles from Lakeba of the Lau Group, Fiji Islands (#1 = cast of right mandible fragment, #2 = left mandible fragment).
[2]Observations recorded by Spennemann (1985) on Burial AK from Shell Midden To.1, Pea, Tongatapu.

* According to Spennemann (1985:19) the lower jaw is 'rocker' but not of the extreme category.
** median-bilateral-angle.
*** bilateral-angle.

Table 6. Natunuku tooth measurements (in mm).

	Mesial	Mesial-distal	Buccal-lingual
Maxillary	Right M2	10.1	12.3
Mandibular	Right C	6.5	7.7
Mandibular	Right I2	5.5	6.2
Mandibular	Left I2	5.7	6.2
Mandibular	Left C	7.3	7.9

Table 7. Mesiodistal and buccolingual crown diameters of permanent mandibular canine teeth for males (in mm).

Sample/size	Side	Mesiodistal	Buccolingual	Source
Natunuku	R	6.50	7.70	(present study)
(n=1)	L	7.30	7.95	
Hawaii		7.15	8.32	(Snow, 1974:93)
(n=24)				
China		7.31	7.89	(Moorrees, 1957)
(n=209)				
Japan		7.00	7.70	(Moorrees, 1957)
(n=146)				

Table 8. Mesiodistal and buccolingual crown diameters of permanent mandibular lateral incisors for males (in mm).

Sample/size	Side	Mesiodistal	Buccolingual	Source
Natunuku	R	5.55	6.15	(present study)
(n=1)	L	5.70	6.15	
Hawaii		6.11	6.82	(Snow, 1974)
(n=23)				
China		6.15	–	(Moorrees, 1957)
(n=187)				
Japan		6.00	–	(Moorrees, 1957)
(n=136)				

Table 9. Mesiodistal and buccolingual crown diameters of permanent maxillary second molar teeth for males (in mm).

Sample/size	Mesiodistal	Buccolingual	Source
Natunuku	10.10	12.30	(present study)
(n=1)			
Tongan Lapita*	12.30	10.90	(Spennemann, 1985:28)
(n=1)			
New Zealand Maori	10.19	11.98	(Dennison, 1979:125)
(n=21)			
Hawaii	10.69	12.09	(Snow, 1974:93)
(n=25)			
Japan	9.80	11.60	(Moorrees, 1957)
(n=142)			
China	9.36	11.00	(Moorrees, 1957)
(n=76)			

* the two measurements as reported by Spennemann would appear to be reversed.

Table 10. Infracranial measurements recorded in the Natunuku skeleton.

	Right	Left
Humerus		
Shaft segment-2 length (Steele, 1970)	215	–
Max. length (M-1)[1]	(290.7)[2]	–
Max. diameter mid-shaft (M-5)	22	–
Min. diameter mid-shaft (M-6)	20	–
Max. diameter deltoid (M-6a)	26.5	–
Shaft circumference (M-7a)	73	–
Radius		
Prox. sagittal diam. (M-5)	15	–
Prox. trans. diam. (M-4)	13	–
Shaft circumference (M-5(5))	45	–
Ulna		
Dorsoventral diameter (M-11)	12.5	–
Transverse diameter (M-12)	19.0	–
Femur		
Shaft segment-2 length (Steele, 1970)	250	253.0
Max. length (M-1)	(444.0)	(446.6)
Anterior posterior diam.-subtroch. (M-10)	26	26
Medio-lateral diam.-subtroch (M-9)	32	32
Anterior-posterior diam.-midshaft (M-6)	32	31
Medio-lateral diam.-midshaft (M-7)	25	25
Bowing (Schofield, 1959:95)	9	7
Tibia		
Shaft segment-3 length (Steele, 1970)	187	–
Maximum length (M-1a)	(393.9)	–
Anterior-posterior diam.-nut. for. (M-8a)	36	34
Medio-lateral diam.-nut. for. (M-9a)	23	23
Anterior-posterior -midshaft (M-8)	33	31
Medio-lateral diam.-midshaft (M-9)	22	20
Patella		
Thickness (M-3)	–	19
Lunate		
Maximum length (M-1)	1.96	1.95
Maximum breadth (M-2)	1.35	1.35
Maximum height (M-3)	2.01	2.05
Trapezium		
Maximum thickness (T-1)[3]	–	1.23
MC-1 articular breadth (M-4)	–	1.75
MC-1 articular height (M-5)	–	2.47
Trapezoid		
Maximum length (M-1)	1.35	–
Maximum breadth (M-2)	1.62	–
Maximum height (M-3)	1.98	–
Hamate		
Maximum height (M-3)	–	2.65
Articular length (M-1)	–	2.01
MC-4/5 articular breadth (M-8)	–	1.31
Capitate		
Articular length (M-4)	2.33	–
Maximum breadth (M-2)	1.39	–
Maximum height (M-3)	1.77	—

Table 10 (cont'd).

	Hand Phalanges Proximal		
	Left thumb	#1	#2
Length (M-1)	3.15	4.25	4.34
Height (M-3)	0.67	0.67	0.66
Breadth (M-2)	0.99	1.04	1.01

	Middle			
	#1	#2	#3	#4
Length (M-1)	2.79	2.87	2.56	1.89
Height (M-3)	0.51	0.66	0.55	0.41
Breadth (M-2)	0.83	0.88	0.86	0.72

	Distal		
	#1	#2	#3
Length (M-1)	1.91	1.95	1.83
Height (M-3)	0.39	0.36	0.36
Breadth (M-2)	0.54	0.50	0.41

[1]Measurements defined in Martin & Saller (1957).
[2]Values within parentheses indicate measurements were estimated from shaft fragments-see text.
[3]Measurement described in Trinkaus (1978).

Table 11. Infracranial indices* and stature** for the Natunuku skeleton.

	Right	Left
Humeral index of robustness (at deltoid)	25.1	–
Humeral diaphyseal index	90.9	–
Crural (tibia-femur) index	88.7	–
Femur-humeral index	65.5	–
Femoral index of robustness	13.3	12.8
Pilastric index	128.0	124.0
Platymeric index	81.2	81.2
Bowing (femur) index	1.5	2.0
Tibial thickness index	66.7	64.5
Platycnemic index	63.9	67.6

*See Table 2 for explanation.

**Stature Estimation using Houghton *et al.* (1975:333) equations:
(1)2.137(444.0) - 5.184(10) + 830.7 ± 31.4 mm = 1727.7 ± 31.4 mm. or approx. 5'8"
(2)2.210(393.9) - 5.247(10) + 978.6 ± 9.4 mm = 1796.6 ± 9.4 mm. or approx. 5'10"
(4)1.782(290.7) - 7.339(10) + 1226.4 ± 56.8 mm = 1671.0 ± 56.8 mm. or approx. 5'6"

Table 12. A comparison of infracranial indices and stature for a number of Pacific groups.

	Natunuku	Fiji(1)	New Guinea (2) Nebira	Tonga(3)	Marquesas(4)	Hawaii(5) Anaehoomalu	Hawaii(6) Mokapu	New Zealand(7)	Easter Island(8)
Crural index	88.7	84.2	84.0	83.5	82.0	84.0	82.1	82.4	83.7
Pilastric index	128.0	133.7	121.0	116.9	122.2	115.0	119.2	116.7	115.8
Platymeric index	81.2	94.5	82.0	84.8	76.5	71.0	71.6	65.0	72.7
Femoral index of robustness	13.3	13.1	13.5	12.6	13.3	14.6	12.4	12.4	12.0
Platycnemic index	63.9	66.7	65.0	66.1	69.4	66.0	66.8	–	71.8
Humeral-femur index	65.5	72.5	70.0	70.3	72.9	72.0	72.5	71.8	71.2
Stature	172.7	169.0	167.0	176.0	174.0	172.7	172.0	171.0	173.0

[(1) Weber (1934); (2) Pietrusewsky (1976); (3) Pietrusewsky (1969a); (4)Pietrusewsky (1976); (5) Pietrusewsky (1971); (6) Snow (1974); (7) Houghton (1980); Schofield (1959); (8) Murrill (1968)]

*for the purposes of this table stature estimates were standardised using formula no. 1 in Houghton *et al.* (1975).

Table 13. Means and standard deviations for seven mandibular measurements recorded in seven male samples (mm).

		INFMANDL		SYMPHYHT		SYMPHYBH		MENFORBH	
Group*	(n)	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
TONGA	13	65.00	6.28	30.00	2.48	14.08	1.75	11.62	0.77
WAIRAU	7	64.71	4.92	34.14	2.73	14.57	0.98	12.42	1.13
CHATHAM	6	65.33	4.84	37.67	1.86	16.50	1.22	12.83	0.75
LAKEBA	1	64.00		28.00		14.00		11.00	
NAMU	14	64.21	4.06	30.14	2.25	14.21	1.89	10.71	1.86
NATUNUKU	1	68.00		26.00		14.00		11.00	
NEWZEA	23	64.39	5.43	33.74	2.68	14.22	1.93	12.35	1.67

n = number of mandibles

* TONGA = 'Atele Mound Burials (1200 B.P. - 390 ± 110 yrs. B.P.) excavated by Davidson (1969) on Tongatapu, Tongan Islands; WAIRAU = Wairau Bar, South Island, New Zealand (1150 A.D. - 1450 A.D.); CHATHAM = Moriori mandibles from the Chatham Is. preserved in Dunedin; LAKEBA = cast of right Lapita-associated mandible fragment (500 B.C.) from Lakeba, Lau Group, Fiji Is. excavated by Best (1977); NAMU = skeletal remains dated between 1000 and 1600 yrs A.D. from Taumako Is., Duff Is. excavated by F. Leach; NEWZEA = Maori material preserved in Dunedin.

		CANINEBH		MOLARBH		RAMUSBTH	
Group	(n)	Mean	S.D.	Mean	S.D.	Mean	S.D.
TONGA	13	11.85	0.69	13.31	1.65	36.92	4.57
WAIRAU	7	12.57	1.51	14.71	0.76	38.57	1.72
CHATHAM	6	12.33	1.21	13.67	1.75	38.00	2.61
LAKEBA	1	10.00		13.00		31.00	
NAMU	14	11.43	1.65	12.50	2.24	35.14	3.78
NATUNUKU	1	12.00		13.00		33.00	
NEWZEA	23	12.13	1.58	14.43	1.75	36.65	3.70

n = number of mandibles

Table 14. Means and standard deviations for five mandibular measurements recorded in 18 male samples.

		BIGONIAL		SYMPHYHT		RAMUSHGT		RAMUSBTH		BICONDWD	
Group*	(n)	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
GULF	12	94.0	3.4	29.6	4.5	62.1	7.6	31.6	2.4	114.1	5.4
NEWBRIT	37	98.5	5.7	31.1	3.8	67.0	5.8	36.7	3.2	118.7	5.7
NEWIRE	9	93.4	7.8	29.7	3.8	62.8	5.9	33.3	3.5	114.6	4.9
NEWCAL	30	99.0	8.2	33.3	3.5	69.1	5.2	41.6	3.0	119.8	5.5
VANUATU	35	95.2	4.9	29.9	3.3	63.6	4.6	34.9	2.7	118.4	5.3
LOYALTY	21	101.1	6.1	33.4	2.6	67.5	5.3	40.9	3.5	118.9	4.5
FIJI	8	99.5	6.6	31.6	1.8	60.9	2.7	35.1	2.3	118.6	4.8
NAMU	9	96.8	4.7	29.4	2.0	66.9	7.1	35.0	4.1	120.1	3.7
GUAMAR	24	106.5	7.2	32.8	4.4	65.0	6.0	37.8	3.3	125.2	8.2
TONGA	16	100.5	7.6	30.4	2.3	64.4	7.3	36.3	3.6	125.4	9.2
SOCIETY	14	99.0	5.2	32.5	2.0	60.4	7.7	35.6	3.1	121.7	6.1
MARQUE	9	100.0	4.7	32.4	2.5	61.7	3.9	35.3	4.2	119.4	6.7
EASTER	14	96.9	4.8	31.6	4.0	60.3	6.0	38.5	4.3	122.4	4.4
NEWZEA	33	103.1	5.7	34.1	2.7	68.3	6.5	36.2	3.5	123.6	8.0
CHATHAM	10	110.7	6.0	36.6	2.3	72.5	2.5	38.0	2.4	126.7	5.1
HAWAII	30	103.3	5.5	33.0	3.3	64.9	5.8	37.9	3.9	128.8	7.2
NATUNUKU	1	100.0	–	26.0	–	60.0	–	33.0	–	114.0	–
GILMARSH	7	96.0	7.7	30.9	2.5	64.4	4.6	37.0	2.9	110.4	2.5

n = sample size

* GULF = Gulf District, Papua New Guinea; NEWBRIT = New Britain; NEWIRE = New Ireland; NEWCAL = New Caledonia; VANUATU = Vanuatu (New Hebrides); LOYALTY = Loyalty Is.; FIJI = Fiji Is.; NAMU = Namu, Taumako Is., Duff Group; GUAMAR = Guam, Saipan and Tinian Is.; TONGA - 'Atele prehistoric burial mounds on Tongatapu, Tongan Is.; SOCIETY = Tahiti and Tuamotu Is.; MARQUE = Marquesas Is.; EASTER = Easter Is.; NEWZEA = New Zealand Maori; CHATHAM = Chatham Is., Moriori; HAWAII = Mokapu, Oahu, Hawaiian Islands; GILMARSH = Gilbert and Marshall Is.

Table 15. Frequency of occurrence of three non-metric mandibular traits for 31 male samples[1].

	Mylo-hyoid bridging		Multiple mental foramina		Rocker jaw	
	n/N		n/N		n/N	
Lapita[2]	0/3	.00	0/5	.00	4/4	1.00
Tonga[3]	5/36	.14	3/36	.08	11/18	.61
Society	2/46	.04	3/46	.07	21/23	.91
New Zealand	3/27	.11	5/28	.18	12/14	.86
Chatham Is.[3]	2/16	.12	2/16	.12	8/8	1.00
Easter Is.	3/32	.09	7/34	.21	14/17	.82
Marquesas[4]	3/23	.13	1/25	.04	12/12	1.00
Wairau Bar[3]	0/19	.00	0/25	.00	11/12	.87
Hawaii	5/90	.06	2/92	.02	40/46	.87
Tinian-Saipan	2/22	.09	4/24	.17	7/10	.70
Gilbert-Marshall[5]	0/12	.00	0/12	.00	6/6	1.00
Namu[3]	0/20	.00	1/20	.05	4/10	.40
Vanuatu	0/16	.00	1/34	.03	11/17	.65
New Caledonia	7/59	.12	11/59	.19	15/30	.50
Loyalty[6]	1/56	.02	6/56	.11	8/28	.29
Solomon Is.	2/42	.05	4/42	.10	18/19	.95
Admiralty	2/29	.07	4/30	.13	9/13	.69
New Ireland	1/43	.02	5/44	.11	14/18	.78
New Britain	16/129	.12	25/130	.19	35/65	.54
Gulf District	1/132	.01	10/126	.08	59/61	.97
Sepik	0/33	.00	3/34	.09	15/17	.88
Fiji[5]	8/26	.31	0/13	.00	10/13	.77
China	2/37	.05	5/74	.07	27/37	.73
Japan	0/104	.00	12/104	.12	35/52	.67
S.E. Asia	4/112	.04	9/114	.08	42/67	.63
Philippines	2/24	.08	1/24	.04	10/12	.83
Sulu	2/32	.06	2/34	.06	13/17	.76
S. Moluccas	0/26	.00	4/26	.15	8/12	.67
Lesser Sundas	0/30	.00	4/34	.12	12/17	.71
Borneo-Celebes	10/90	.11	7/92	.08	40/45	.89
Java	5/148	.03	13/148	.09	55/74	.74

[1] Except for those cases indicated below, these data are taken from Pietrusewsky (1984).
[2] This sample combines data on the Lapita-associated mandibles presented in Table 5.
[3] These samples correspond to those used in the multivariate analysis of mandibular measurements (Pietrusewsky, 1985b).
[4] This sample consists solely of mandibles from the prehistoric Hane Dune site described by the author (Pietrusewsky, 1976).
[5] Data recorded on Fijian mandibles are from Pietrusewsky (1969a).
[6] These samples are taken from Pietrusewsky (1977).

Appendix B

Inventory of major human bone fragments identified in the Natunuku material.

Skull
- Right mandibular fragment
- Right zygomatic bone fragment
- Frontal fragment (left side)
- Occipital bone fragment

Dentition
- 5 isolated teeth (upper right M2, lower right and left C, right and left I2)

Thorax
- Fragment of left scapula (glenoid cavity)
- Rib fragments
- Vertebrae fragments

Right arm
- Humerus shaft
- Radius: proximal end of shaft
- Ulna shaft fragment

Right hand
- Carpals: hamate, lunate, triquetrum
- Metacarpals: MC-3 (proximal end missing)
- Phalanges: 2 proximal (for MC-2 and 3); 2 middle (for MC-3 and 4)

Left arm
- Humerus: small fragment from head region
- Radius: distal shaft
- Ulna: distal shaft

Left hand
- Carpals: capitate, trapezium, lunate
- Metacarpals: MC-1 (distal fragment); MC-2 (extremities missing); MC-3 (distal extremity missing)
- Phalanges: proximal and distal phalanges for thumb; one proximal fragment (for MC-3); 4 middle phalanges (for MC 2-5); 2 distal phalanges (for MC 3 and 4).

Pelvis
- small fragments

Right leg
- Femur: shaft fragment
- Tibia: shaft fragment
- Fibula: shaft fragment

Left leg
- Femur: major shaft fragment and small head fragment
- Tibia: major shaft fragment
- Fibula: major shaft fragment
- Patella: fragment

The Lapita-associated Human Material from Lakeba, Fiji

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ABSTRACT. The remains of an individual interred about the middle of the first millenium BC, in association with Lapita ceramics, on the island of Lakeba in the Lau group of Fiji, have been examined. The long bones were robust and showed marked bowing and other evidence of considerable muscularity. The femur had an oval fovea and marked platymeria (index 71). Stature was estimated at 1,715 mm. The incomplete jaw was of 'rocker' form on one side and showed a very slight antegonial notch on the other. The morphology of this individual is fully compatible with the known Polynesian skeletal phenotype.

HOUGHTON, P., 1989. The Lapita-associated human material from Lakeba, Fiji. Records of the Australian Museum 41(3): 327–329.

Human remains associated with typical Lapita ceramics have been excavated on the island of Lakeba in the Lau group of Fiji (Best, 1984). The material was greatly fragmented, but a useful assessment of phenotypic affinities was possible for one individual (from Site 196: trench 28). Carbon-14 dates for the initial occupation of the site early in the first millenium BC indicate interment towards the middle of that interval (Best, 1984: 100–105).

Material

The remains were of an adult male, probably in the fourth decade of life (30 to 40 years). The long bones were robust (though a defined robusticity index was not obtainable) and with physiologically bowed shafts to accommodate a considerable musculature. The maximum length of the intact right radius was 245 mm, and of the right ulna 266 mm. Derived stature estimates using different equations are given in Table 1. The Polynesian equations of Houghton *et al.* (1975) gave the mid-estimates and also the least range; a stature of 1,715 mm is suggested. The upper femoral shafts were markedly flattened with a platymeric index of 71, rather greater than that found in the prehistoric Maori (Schofield, 1959) but similar to prehistoric Hawaii (Snow, 1974). The femoral heads showed distinct oval foveae (Fig.2). The forearm bones showed the marked bowing characteristic of Polynesians and the humeri showed prominent deltoid tuberosities. The spine was represented by several vertebrae from neck to lumbar region. It showed very little degeneration compared with prehistoric New Zealanders of the same age, where lumbar and cervical degeneration are often very advanced by the mid-30s. Clavicles show first-rib grooves, right more than left, suggesting regular canoe paddling. The right upper limb bones are slightly more robust than the left and this individual was thus presumably right-handed.

The cranial fragments offered little information, but the mandibular body and about half of each ramus were present. This bone was not particularly robust, though function would have been influenced by extensive dental caries in both jaws. The mandible verged on the rocker form, the right side displaying no antegonial notch and

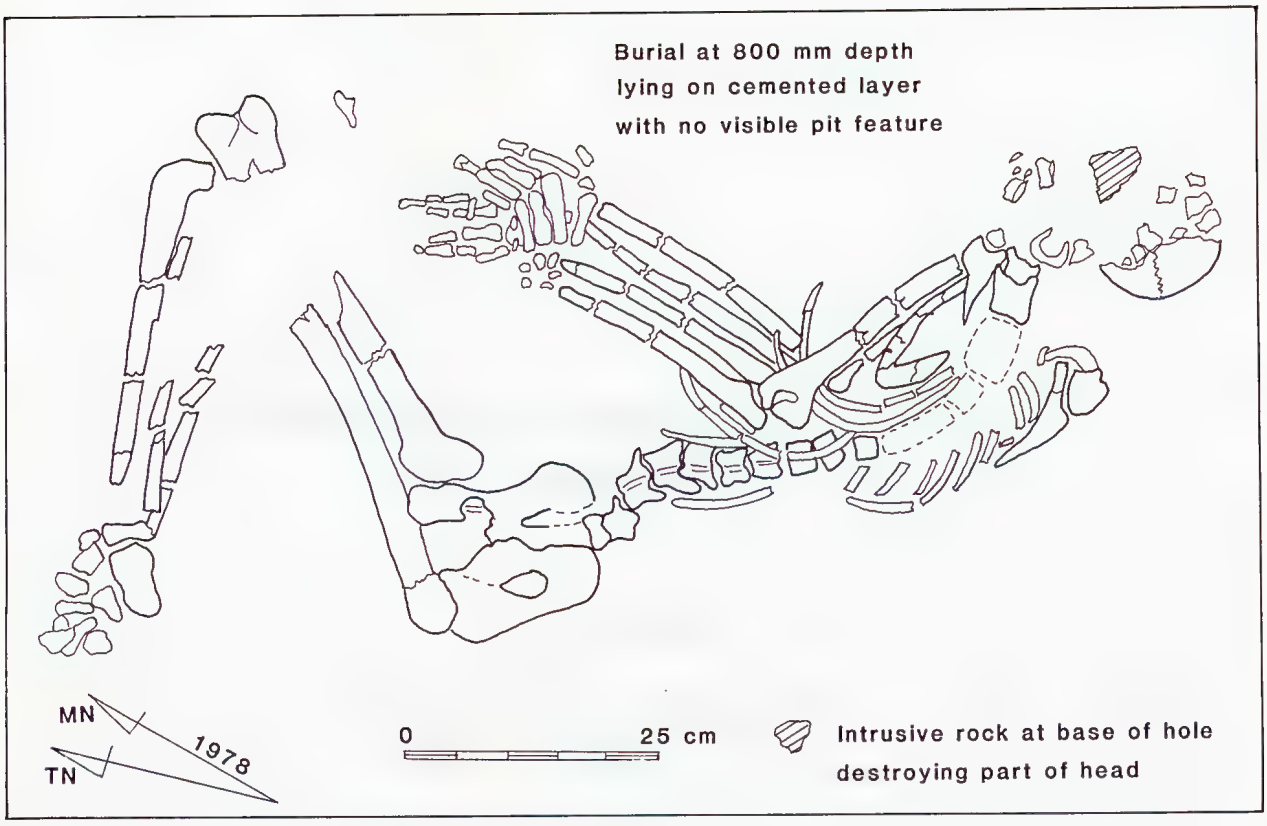

Fig.1. Burial at 800 mm depth resting on a cemented layer of grey-orange sand, Trench 28, Site 101/7/196, Wakea, Lakeba, Lau Group, Fiji (from Best, 1984).

Fig.2. Casts of: a. right and left mandibular fragments; the antegonial notch is absent on the right side and minimal on the left. b. femoral head showing the oval fovea.

Table 1. Stature estimates in millimetres from maximum lengths of right radius and right ulna using equations derived from Polynesian (Houghton *et al.*, 1975), White American (Trotter, 1970), and Mongoloid (Trotter, 1970) body proportions.

	Mongoloid	Polynesian	White American
radius 245 mm	1687	1711	1720
ulna 26mm	1700	1716	1735

the biological significance of this feature see Houghton & Kean, 1987).

Some features of the dentition were preserved. The lower third molars were congenitally absent and it could be ascertained that the upper left third molar had erupted. An upper central incisor showed moderate shovelling both lingually and labially, while a lateral incisor showed a trace of shovelling. A lower second molar showed a five-cusped, Y-fissure morphology. Five upper and nine lower teeth could be measured (Table 2).

Table 2. Tooth dimensions in millimetres. The teeth are defined according to the FDI system.

Tooth	mesiodistal	buccolingual
11	8.6	8.3
12	6.5	6.9
13	8.4	9.2
23	8.5	9.0
27	10.5	11.7
31	5.7	6.9
32	5.9	6.8
33	7.5	8.0
34	8.4	9.0
37	12.1	10.8
41	5.7	6.8
42	6.0	7.0
43	7.4	8.5
44	8.1	9.1

This array of skeletal features, and the stature estimate, are distinctively Polynesian. Indeed, the femur takes the more extreme morphology of eastern Polynesia. I have tended to think of the latter as arising by succesive processes of genetic drift and reduction of the gene pool with eastward migration across Polynesia, but there is evidence here that the form was established earlier in the west. Like the bowing of the long bones it may be an indicator of a substantial thigh musculature and thus a large lean body mass. These are characteristics in harmony with the oceanic environment and Bergmann's Law (Houghton, in press).

I do not think the limited dental data merit comparative statistical analysis. The aplastic third molars and incisal shovelling accord with Polynesian morphology (e.g. Snow, 1974, Suzuki & Sakai, 1964).

These remains were subsequently returned to Lakeba for reburial. Casts were made of the dentition and mandibular and femoral fragments, and are retained in the Department of Anatomy, University of Otago.

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Comment on the Human Skeletal Material from Pea, Tonga, Site To.1

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ABSTRACT. Some pathological features evident in the human skeletal material from the Lapita site at Pea, Tonga, Site To.1, are reinterpreted. Some reordering of the remains between individuals is suggested, and previous suggestions that there is evidence of either metastatic carcinoma or early Pagets disease in the cranial vault are not supported.

HOUGHTON, P., 1989. Comment on the human skeletal material from Pea, Tonga, Site To.1. Records of the Australian Museum 41(3): 331–332.

This Lapita-associated material excavated by Poulsen (1987) has been exhaustively analysed by Taylor (1987) and Spennemann (1987). The comments here relate to some contentious points, mainly of pathology, and should be read against the previous analyses.

Material

1. Mandible. The right mandibular condyle has been broken off post-mortem, but sufficient neck remains to indicate that some abnormality was present in this region during life though whether congenital or pathological (trauma or infection) cannot be said (Fig.1). A cranial fragment bearing the right temporomandibular joint surface is preserved and shows the articular eminence to have been largely obliterated, with formation here of a new, rough-surfaced fossa. The mandible thus probably belongs to at least some of the cranial fragments.

2. The maxillary fragment shows a more advanced and carious pathology than does the mandible (Fig. 2), and a considerably larger dental arch. Even allowing for mesial drift of the lower teeth as a result of long-standing loss of the incisors, it seems the arches are incompatible.

3. From (1) and (2) above, it follows that the maxillary fragment is probably from another individual, with the mandible belonging to the main individual. This is different from the picture presented by Spennemann (1987), though it must be said that a decision either way is of no great moment.

4. The mandibular pathology, which would influence function and musculature, renders its morphology unsuitable for determining biological relationships.

5. The cervical spine has been said to show "remarkably severe" osteoarthritis (Spenneman, 1987). Chapman (1972) gives a reasonably objective grading for vertebral degeneration, and on her criteria I would grade these changes as slight to moderate. It is to be noted that osteoarthritis occurs only in synovial joints, and is not applicable to the joints between vertebral bodies.

6. It has been suggested that the cranial vault shows evidence either of metastatic carcinoma or early Pagets disease (Spenneman, 1987). I find no evidence of metastases, though there are some normal depressions of meningeal origin (arachnoid villi). The vault structure lies

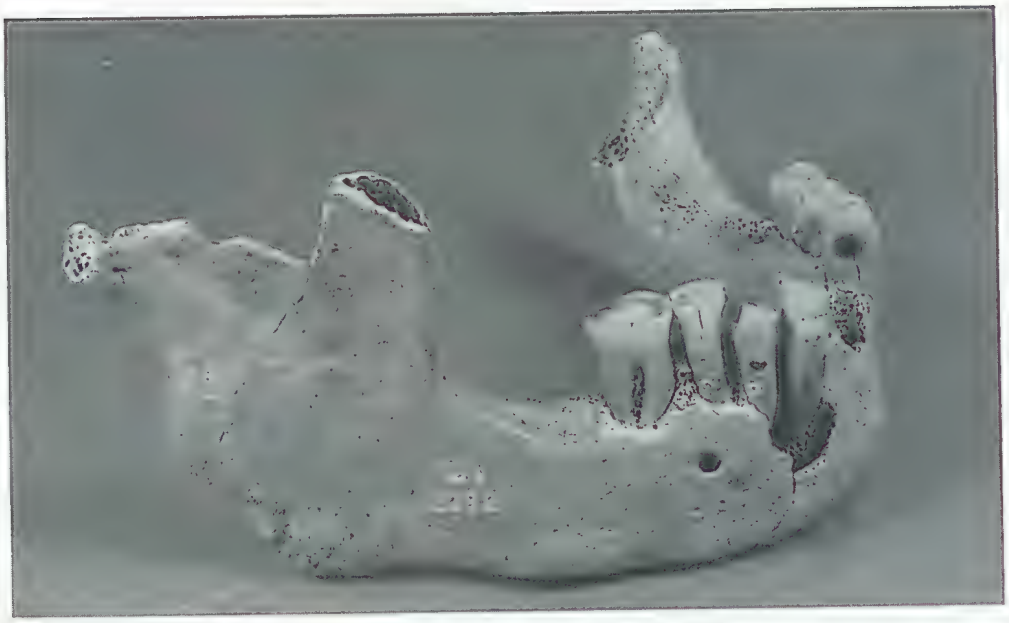

Fig.1. Mandible, showing an expanded and pathological right condylar neck. Most of the actual condyle has been broken post-mortem.

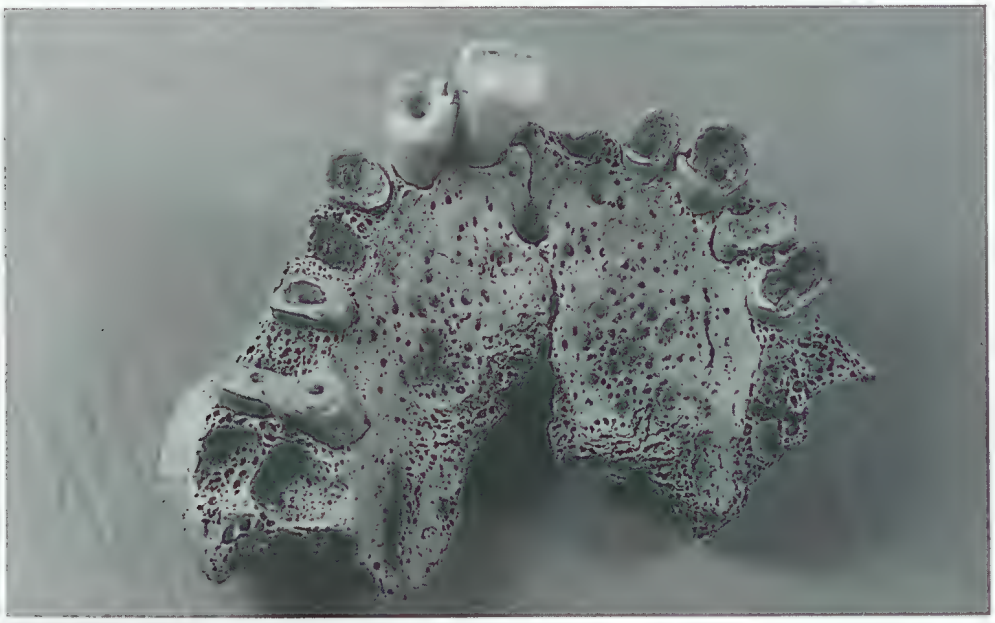

Fig.2. Palatal view of maxillary fragment showing dental pathology.

within the considerable normal range, and does not show Pagets disease.

7. There are two well-healed rib fractures.

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